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NNECTICUT ACADEMY OF ARTS AND SCIENCES
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The American Species of Marchantia

BY

ALEXANDER W. EVANS

NEW HAVEN, CONNECTICUT

1917

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I. INTRODUCTION

The genus *Marchantia* is almost world-wide in its distribution and includes some of the largest and most conspicuous of the Hepaticae. According to the current rules of nomenclature the genus was not definitely established until 1753, when Linnaeus published it in the first edition of his Species Plantarum, but the use of the name *Marchantia* dates from the year 1713. Linnaeus recognized seven species, only the first two of which, *M. polymorpha* and *M. chenopoda,* are now retained in the genus. The type species, *M. polymorpha,* he cites from Europe only, and gives Martinique as the habitat of *M. chenopoda.* At the present time *M. polymorpha* is known to be almost cosmopolitan, while the range of *M. chenopoda,* although apparently restricted to tropical America, is likewise very extended.

For a long time *M. polymorpha* was the only species recognized in Europe. In 1817, however, a second species, *M. paleacea,* was described by Bertolini[1] from material collected in Italy. This species had been distinguished and figured by Micheli[2] nearly a century earlier but had not been accepted by Linnaeus. It is now known to have a wide distribution in tropical and subtropical regions, its range extending far beyond the confines of Europe. Other European species which have been proposed from time to time, such as *M. macrocephala* Corda and *M. Sykorae* Corda, have never received wide acceptance and undoubtedly represent mere forms of *M. polymorpha.*

The history of the genus in America, when the entire continent is considered, is very much involved. This is due partly to the full representation of the genus and partly to the confusion which has arisen in the interpretation of certain species. Before the publication of Gottsche, Lindenberg and Nees von Esenbeck's Synopsis Hepaticarum, in 1847, the following species of *Marchantia* had been recorded from North and South America: *M. papillata* Raddi (1823) from Brazil, *M. platycnemos* Schwaegr. (1827) from Brazil, *M. Swartzii* Lehm. & Lindenb. (1832) from Jamaica, *M. squamosa* Raddi (1832) from Brazil,

[1] Opus. Sci. Bologna 1 : 242. 1817.

[2] Nova Plant. Gen. 2. *pl. 1, f. 4.* Florence, 1729.

M. cartilaginea Lehm. & Lindenb. (1832) from St. Vincent, *M. brasiliensis* Lehm. & Lindenb. (1832) from Brazil, *M. Berteroana* Lehm. & Lindenb. (1834) from Juan Fernandez, *M. domingensis* Lehm. & Lindenb. (1834) from Santo Domingo, *M. tholophora* Bisch. (1835) from Mexico, *M. inflexa* Mont. & Nees (1838) from Martinique, *M. plicata* Nees & Mont. (1838) from Bolivia, *M. quinqueloba* Nees (1838) from the West Indies,[3] *M. peruviana* (Nees & Mont.) Nees (1839, as *Grimaldia peruviana*) from Bolivia. In the Synopsis Hepaticarum these species are all recognized with the exception of *M. Swartzii,* which is made a synonym of *M. chenopoda,* and *M. platycnemos,* which is made a synonym of *M. papillata.* Two other species, *M. pusilla* Nees & Mont. from Chile and *M. lamellosa* Hampe & Gottsche from Venezuela, are described as new; a third species, *M. linearis* Lehm. & Lindenb. (1832), originally described from Nepal, is quoted from several of the Lesser Antilles; while both *M. polymorpha* and *M. chenopoda* are cited from numerous American localities. The Synopsis, therefore, recognizes sixteen species in all from North and South America.

During the period from 1847 to 1899 comparatively little was added to our knowledge of the genus in America. The following species, however, were described as new: *M. flabellata* Hampe (1847) from Venezuela, *M. Notarisii* Lehm. (1857) from Chile, *M. Dillenii* Lindb. (1883) from Jamaica, *M. subandina* Spruce (1885) from Peru, *M. Bescherellei* Steph. (1888) from Brazil, and *M. oregonensis* Steph. (1891) from Oregon. Two of the most noteworthy papers on *Marchantia* appearing during this time were by Schiffner. In the first he brought out the fact that *M. brasiliensis* and *M. cartilaginea* were synonyms of *M. chenopoda*[4]; in the second he showed that *M. tabularis* Nees, a South African species, was a synonym of the older *M. Berteroana.*[5] Another reduction to synonymy was suggested by Howe,[6] who showed that *M. oregonensis* was based on very uncertain characters and that it could not be well separated from *M. polymorpha.*

[3] No station is cited for this species in the original publication; the Synopsis, however, gives, "in India occidentali."

[4] Nova Acta Acad. Leop.-Carol. 60: 287, 288. 1893.

[5] Oesterr. Bot. Zeitschr. 46: 41-44, 100-103. 1896.

[6] Mem. Torrey Club 7: 62. 1899.

In 1899 Stephani[7] published his monograph on *Marchantia* in the first volume of his Species Hepaticarum. He describes eighteen species in all from America, six of which are confined to North America and eight to South America. Of these eighteen species *M. Elliottii* of Dominica and *M. caracensis* of Venezuela and Mexico are described as new, while *M. cephaloscypha* Steph. (1883), originally described from New Zealand, is quoted from Chile and Patagonia. He accepts Schiffner's reduction of *M. cartilaginea* to synonymy but maintains both *M. brasiliensis* and *M. oregonensis* as valid. Under *M. tabularis* he cites *M. Berteroana* as a synonym (on the authority of Schiffner) but gives no American localities. Under *M. domingensis* he gives *M. inflexa* as a synonym and states further that the American stations for *M. linearis* (as given in the Synopsis) belong to *M. domingensis* instead. He includes *M. Dillenii* among the synonyms of *M. chenopoda* and considers that *M. peruviana* and *M. Notarisii* are very close to this species and may be merely forms of it. Two species recognized by the Synopsis, *M. quinquecloba* and *M. pusilla,* he gives up altogether, because they were based on fragmentary specimens, and he makes no mention whatever of *M. flabellata.*

If *M. Berteroana* is reinstated as an American species and if *M. flabellata* is added, Stephani's total of eighteen species would still be maintained, even if *M. brasiliensis* and *M. oregoncnsis* are considered synonyms. It will be seen that this total is scarcely different from the total of sixteen species given in the Synopsis Hepaticarum. The writer hopes to show, however, that these numbers are much too high and that further reductions to synonymy are necessary. In his opinion there are only nine species based on characters which seem trustworthy, and it is possible that two of these will not be considered distinct when they become more fully known. There remain five species which are doubtful, either because the published descriptions are incomplete or because the original material is immature or fragmentary. Two of these, as noted above, are discarded altogether by Stephani, and it is probable that the other three deserve the same fate. The doubtful species, however, will be alluded to briefly at the close of the paper.

[7] Bull. Herb. Boissier 7 : 383-407, 518-533. 1899.

II. MORPHOLOGICAL NOTES ON THE GENUS

No other liverwort has been so much discussed and described as *Marchantia polymorpha*. According to Lindberg[1] it attracted the attention of naturalists at a very early date and was known to both Aristotle and Theophrastus. Within more recent times it has repeatedly been the subject of morphological researches and has served in numerous text books as a typical representative of the thallose Hepaticae. Over eighty years ago Mirbel[2] published the first extensive account of its morphology. He brought out the essential features of the thallus and of its various tissues and gave a clear description of the receptacles and the gemmae. Of the later works dealing with the morphology of the species those by Leitgeb,[3] Kny,[4] Ikeno,[5] and Durand[6] may be particularly mentioned. The first two deal with the plant in a general way, very much as Mirbel's memoir did, although they include many original observations. The last two are much more specialized and deal with the cytology and development of the reproductive organs. Although *M. polymorpha* itself has been treated so exhaustively the other species of the genus have been but little studied by morphologists. In one of his earlier papers Schiffner[7] published a series of interesting observations on the Javan *M. geminata* R. Bl. & N.; but aside from this,

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[1] Hepat. Utveckling 15. Helsingfors, 1877.

[2] Recherches anatomiques et physiologiques sur le *Marchantia polymorpha*. Mus. Hist. Nat. Nouv. Ann. 1:92-130. *pl. 5-7.* 1832. For a reprint of this paper, with a few slight alterations, and a Complément des observations sur le *Marchantia polymorpha,* see Mém. Acad. Sci. 13:337-436. *pl. 1-8.* 1835. For a translation into German by Von Flotow, see Nees von Esenbeck, Naturg. Europ. Leberm. 4:445-494. Breslau, 1838.

[3] Unters. über Leberm. 6:114-123. *pl. 9.* Graz, 1881.

[4] Bau und Entwickelung von *Marchantia polymorpha* L. Bot. Wandtafeln 364-401. *pl. 84-90.* Berlin, 1890.

[5] Beiträge zur Kenntnis der pflanzlichen Spermatogenese: Die Spermatogenese von *Marchantia polymorpha.* Beih. Bot. Centralbl. 15:65-88. *pl. 3 + f. 1.* 1903.

[6] The development of the sexual organs and sporogonium of *Marchantia polymorpha.* Bull. Torrey Club 35:321-335. *pl. 21-25.* 1908.

[7] Ueber exotische Hepaticae. Anhang I. Morphologische Bemerkungen über *Marchantia.* Nova Acta Acad. Leop.-Carol. 60:279-284. *pl. 19.* 1893.

records of morphological importance are mostly in the form of scattered notes, and these are often to be found in taxonomic treatises.

In the present paper the morphology of *Marchantia* will be treated largely from the standpoint of the taxonomist. In other words the parts of the plant which yield the most distinct and constant specific characters will be primarily considered. These parts include the epidermis and the epidermal pores, the compact ventral tissue, the ventral scales, the rhizoids, the receptacles, and the cupules. The photosynthetic layer, the sexual organs, and the sporophyte, although yielding important generic characters, are less helpful when the individual species are considered. For the sake of completeness, however, a brief account of the sporophyte will be included.

The flat thallus of *Marchantia* is of the usual prostrate dorsiventral type and branches repeatedly by forking. It varies considerably in size and in thickness in certain species, so that measurements of its various dimensions have to be employed with caution. At the same time some of the species are distinctly larger than others. The growth of the thallus is normally unlimited until the sexual branches or receptacles (see FIG. 9, A, B) are produced. These represent the erect prolongations of prostrate branches and are limited in growth. The inflorescence is dioicous throughout the genus. Vegetative reproduction is carried on by means of discoid gemmae, which may be formed on either male or female individuals and which apparently do not interfere with the growth of the plant.

The thallus shows clearly the usual differentiation into an epidermis, a photosynthetic layer and a compact ventral tissue bearing scales and rhizoids. The photosynthetic tissue consists of a single layer of large air-chambers separated from one another by continuous plates of cells. Each air-chamber is connected with the outside by a single pore in the epidermal roof. From the floor of the chamber arise numerous short rows of green cells, subspherical in form and freely exposed to the air of the chamber. The rows, which are simple or branched, are mostly from two to five cells long and the uppermost cells, except in the vicinity of the pore, are usually attached to the epidermis. The air-chambers vary greatly in size, not only in different species but often in different parts of an individual thallus.

1. Epidermis and Epidermal Pores

The ordinary epidermal cells are fairly uniform throughout the genus and it is doubtful if they offer any very trustworthy differential characters. Their size often varies markedly on an individual thallus and may be directly affected by differences in external conditions. Although the cells are usually colorless or pale they sometimes produce chloroplasts in abundance. In the majority of cases they are arranged in a single layer, but in certain species at least, such as *M. chenopoda* (Fig. 19, E) and *M. palcacea* (Fig. 8, D), the epidermis may be two cells thick in parts of its extent. The walls may vary considerably in thickness, but they are rarely very firm and are destitute of distinct trigones.

Cells containing oil-bodies, cells containing slime, and minute surface papillae are sometimes found in the epidermis. The cells containing the oil-bodies are usually distinctly smaller than the neighboring cells and are easily distinguished by their granular contents, which nearly or quite fill the cell cavities. In *M. chenopoda* these cells are not infrequent and do not seem to be restricted to any definite part of the thallus; in *M. polymorpha* they occur near the margin and seem to be absent elsewhere; while in certain other species there are apparently no cells of this character in the epidermis.

Epidermal cells containing slime are, according to our present knowledge, restricted to *M. chenopoda.* The slime-cells are scattered about in the epidermis and always occur in regions where the epidermis is two cells thick, being situated in the inner layer (Fig. 19, L). They are much larger than the surrounding epidermal cells and strongly compress those of the outer layer. When a piece of the epidermis is examined from above the slime cells are seen to be covered over by these compressed cells. Apparently Voigt[8] was the first to observe the slime-cells, although he failed to recognize their true character. The much larger slime-canals in *Conocephalum conicum* (L.) Dumort. were soon afterwards described by Goebel,[9] and Leitgeb[10] pointed out that the slime-cells of *M. chenopoda* were of the same

[8] Bot. Zeit. 37 : 733. 1879.
[9] Arb. Bot. Inst. Würzburg 2 : 531. 1880.
[10] Unters. über Leberm. 6 : 16. 1881.

nature. He showed that they occurred not only *under* the epidermis, as he expressed it, but also in the compact ventral tissue and in the partitions between the air-chambers, and he emphasized the fact that they were especially abundant in the female receptacles. The distribution of the slime-cells in *Marchantia* was a little later discussed at length by Prescher.[11] He found no trace of them in *M. Berteroana, M. papillata, M. emarginata* R. Bl. & N., or *M. linearis;* he found them restricted to the compact tissue of certain definite regions in *M. polymorpha* and *M. paleacea;* and it was only in *M. chenopoda* (including *M. cartilaginea*) that he found them in the epidermis.

Surface papillae have been figured very accurately by Kny[12] in the case of *M. polymorpha.* They are minute appendages of the epidermis, which are cut off by walls and rounded or bluntly pointed at their free ends (Fig. 2, J, L, O, P). Sometimes a papilla is situated over a single cell and sometimes over the partition between two cells, showing in the latter case that an epidermal cell had divided after the papilla had been formed. Papillae of this type seem to be rare on vegetative branches and confined to certain species. So far they have been reported in two East Indian species, *M. emarginata* and *M. Treubii* Schiffn.,[13] but they seem to be absent from all the American species except *M. polymorpha.* In this last species, as shown by Schiffner,[14] the median portion of the thallus is always free from papillae, while the marginal regions sometimes show them clearly. The distribution is very different, however, in *M. Treubii,* where the papillae are most abundant in the median portion and gradually decrease toward the margins. Whether papillae of this character form a constant feature of any of the species where they have been found is perhaps doubtful. In one specimen of *M. emarginata,* for example, in the writer's collection (Schiffner, Iter Indicum *37*), the plants seem to have developed no papillae, and they are frequently absent from the vegetative branches in *M. polymorpha.* When they occur on receptacles or cupules, as in this same species, they seem to be more constant.

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[11] Die Schleimorgane der Marchantieen. Sitzungsb. Kais. Acad. Wissen. Wien, Math.-naturw. Cl. 86[1]: 132-158. *pl. 1, 2.* 1882.

[12] Bot. Wandtafeln *pl. 84, f. 2, 3.* 1890.

[13] See Schiffner, Fl. de Buitenzorg 4: 32, 35. Leiden, 1900.

[14] Lotos 49: 93. 1901.

The complex epidermal pores of *Marchantia* are of much interest. They are of the dolioform or barrel-shaped type, that is, the opening of the pore is surrounded by two series of cells arranged in concentric rows, one series projecting more or less above the surface of the thallus, the other projecting into an air-chamber. Although pores of this type are found on the sexual branches of most of the Marchantiaceae, the only genera where they occur on the vegetative branches are *Marchantia, Preissia,* and *Bucegia.* Even in *Marchantia,* as shown by Kamerling,[15] immature shoots sometimes produce pores of the simple type found in most of the other members of the group.

The first attempt to utilize the structural features of the pores for taxonomic purposes seems to have been made by Voigt.[16] He studied eight species of the genus, and showed that the number of pores in a given area, the number of rows of cells surrounding a pore, and the number of cells in a row were fairly constant for each species. Stephani also has drawn specific characters from the pores, but certain of his distinctions, as will be shown below, are subject to variation and must be used with caution.

In the case of *M. polymorpha* the pores have been repeatedly figured, although the published illustrations are not all of the same degree of excellence. Among recent figures those by Voigt, Kny, and Müller[17] bring out most of the essential points. According to Voigt, whose account of the pores is unusually full, the opening is surrounded by five circular rows of cells, three belonging to the upper and two to the lower series, but both Kny and Müller state that the upper series is normally composed of only two rows making four rows in all, a statement which agrees with the writer's observations (see Fig. 2, A, B). Under some conditions the number of rows may be reduced to three or even to two. In the upper series each row is composed (in most cases at least) of four cells (Fig. 2, A, B), and immediately surrounding the pore a circular membranous ridge is present, probably representing, as in the simple pores of *Targionia,*[18] a collapsed series of cells. This ridge is shown by Voigt (*f. 1*),

[15] Flora 84 (Ergänzungsb.) : 57. 1897.
[16] Bot. Zeit. 37 : 741. 1879.
[17] Rabenhorst's Kryptogamen-Flora 6 : *f. 187.* Leipzig, 1907.
[18] See Deutsch, Bot. Gaz. 53 : 494. *f. 9.* 1912.

but is not brought out in the figures of Kny and Müller. It is sometimes very narrow and absolutely colorless and can then be demonstrated only with difficulty. In the lower series each row is likewise composed in most cases of four cells, those bounding the inner opening being distinctly differentiated. Their usual appearance is clearly shown by Kny (*pl. 84, f. 2*), each cell being in the form of a narrow, curved, four-sided figure with a rounded median projection extending toward the center of the pore. All the cell-walls immediately bounding the pore are shown covered over with a granular deposit of some resinous substance, which hinders or prevents the entrance of water through the pore. Kny comments on the fact that the pores vary greatly in size and that the projections from the cells bounding the inner opening sometimes meet. In his opinion these projections probably make still more difficult the entrance of water through the pore. This view is upheld by Ruge,[19] who finds the pores almost completely closed by the projections in a submerged form of *M. polymorpha.* In Fig. 2, D-I, some of the variations shown by the cells bounding the inner opening are brought out. In Fig. 2, E, the projections are only slightly developed, although the upper cell on the left approaches the condition portrayed by Kny; in Fig. 2, D, F, I, the projections are well developed but not sharply defined from the rest of the cell; in Fig. 2, G, H, the projections are both well developed and sharply defined. These last figures, drawn from a plant growing in a very wet locality, support the statements of Ruge and agree with the figures published by Müller. The cells drawn, however, seem to be nearly or quite destitute of the resinous deposit so conspicuously shown in the remaining figures and in Müller's figures also.

Although the inner openings of the pores in *M. polymorpha* are subject to so much variation, Stephani insists that important specific characters in the genus *Marchantia* are yielded by the inner openings. He recognizes four types[20] and states that they are not connected by transitional conditions. In the first type the four cells bounding the opening are narrow and not materially changed in shape by increased turgidity, the opening itself exhibiting a quadrate form. In the second type the four bounding

[19] Flora 77: 294. *f. 11.* 1893.

[20] Bull. Herb. Boissier 7: 385. *f. a-d.* 1899.

cells bulge into the opening in the form of rounded projections, the opening itself showing an outline with four strongly concave sides and four sharp angles; by increasing the turgidity this opening can be almost completely closed. In the third type (which is essentially the same as the pores of *Preissia*) the four cells likewise bulge into the opening but the bulging portions are more sharply defined and the opening appears in the form of a four-sided figure with very concave sides but with rounded dilations at the angles; this opening, which Stephani describes as cruciate, can be completely closed by an increase of turgidity. In the fourth type the opening is very large and bounded by many cells (fifteen in Stephani's figure), each cell bulging into the opening in the form of a longer or shorter cylindrical projection, the opening itself thus acquiring a very irregular outline. To the first type Stephani assigns (among others) *M. polymorpha, M. plicata* and *M. domingensis;* to the second type, *M. disjuncta;* and to the third type, *M. cephaloscypha* and *M. paleacea.* The only representative of the fourth type is *M. macropora* Mitt. of New Zealand.

Schiffner,[21] however, had already called attention to the danger of placing too much confidence in the peculiarities of the cells bounding the inner openings. According to his account these cells in most species of *Marchantia* bulge more or less into the opening, the form of which may vary accordingly, and his statements would support the view that there was no sharp distinction between the first and second types of Stephani. Even in *M. Berteroana,* which Stephani would assign to his third type, Schiffner finds only an insignificant modification of the usual condition. He adds that the number of bounding cells in this species, although usually four, may vary from three to six on an individual thallus, and that the walls of the cells commonly lack the resinous deposit found in *M. polymorpha.* Goebel[22] is likewise inclined to recognize a single type of pore in *Marchantia* with respect to the inner opening, and he sees no essential difference between Stephani's fourth type and the others. He expresses no positive opinion on this last point, however, because he had no material of *M. macropora* at his disposal. He considers that the pores are plastic structures, subject to modifica-

[21] Nova Acta Acad. Leop.-Carol. 60: 286. *pl. 19, f. 8. 20.* 1893.

[22] Flora 96: 193. 1906.

tion through external conditions, and he emphasizes the fact that the pores of xerophilous forms can often be more or less completely closed by an increased turgidity of the bounding cells.

It is clear from the observations of Schiffner and Goebel that the pores in *Marchantia* (excepting perhaps in *M. macropora*) conform to one general type and that the distinctions relied upon by Stephani are less constant than he supposed. This is especially well seen in *M. polymorpha,* where the inner opening shows all gradations from a quadrate to a cruciate form and thus exemplifies all three of the conditions upon which the first three of Stephani's types were based. *M. polymorpha,* however, is an exceedingly plastic species and it is doubtful if any of the other members of the genus exhibit the same wide range of variation in the inner opening. Schiffner's figures of *M. geminata,* for example, although illustrating conditions connecting the first and second of Stephani's types, show no approach to the third; while in *M. palcacea,* according to the information at hand, the inner opening is always cruciate and thus does not deviate from the third type. For purposes of taxonomy, therefore, the writer would still consider it expedient to recognize two types of pore among the American species, the distinctions between the types breaking down in the case of *M. polymorpha.* In the first type (which includes Stephani's first and second types) the inner opening is bounded by three to six cells, the usual number being four, and shows all gradations between a polygon, commonly four-sided, with slightly convex sides and one with strongly concave sides and sharp angles. In the second type (which is the same as Stephani's third type) the inner opening is distinctly cruciate with four rays dilated at the apex or, in the rare cases where the number of bounding cells is less or greater than four, with fewer or more rays. Stephani's fourth type, which does not occur in America so far as known, need not be further considered.

As an example of the first type of pore *M. chenopoda* may be selected. In this the opening, as pointed out by Voigt, is surrounded by about seven rows of cells, shown clearly in cross-section (Fig. 19, C-G), four of the rows usually belonging to the upper and three to the lower series. The walls bounding the opening are either smooth or with a resinous deposit. In the upper series (Fig. 19, A, B) the innermost row is usually composed of four narrow cells and the second row of the same num-

ber, but the third row commonly shows twice as many and the fourth row a much larger number. The ridge immediately around the opening is clearly marked. In the lower series (FIG. 19, H-K) the innermost row lies almost directly beneath the second row, so that only the first and third rows show clearly from below. The first and second rows are usually composed of four cells each, the walls bounding the pore being more or less strongly convex. The third row usually contains more cells than the first and sometimes twice as many, but it rarely contains as many as the fourth row of the upper series, where the cells are essentially like the ordinary epidermal cells. Of course the numbers just given are subject to variation, the number of cells bounding the outer and inner openings being often more than four.

As an example of the second type of pore *M. paleacea* may be selected, and the illustrations given in the present paper (FIG. 8, A-H) may be compared with the one published by Müller.[23] The descriptions given by Voigt may likewise be consulted. The cells bounding the pore are usually in six rows, three belonging to each series, and the rows are commonly composed of four cells apiece. The cell-walls bounding the pore are smooth throughout. In the upper series the ridge around the opening is distinct and the cells are very narrow, standing in sharp contrast to the neighboring epidermal cells. In the lower series the cells bounding the inner opening are much broader than the others and project so strongly that they often touch in the center and almost occlude the cruciate opening. Sometimes one or more cells of the second row project also (FIG. 8, D), but the cells of both the second and third rows are usually narrow, resembling in this respect the cells in the upper series.

According to the account given by Kamerling,[24] the size of the inner opening in a pore of the first type is not decreased to any great extent by an increase of the turgidity of the surrounding cells, while in a pore of the second type the decrease is very marked. In his opinion the cells surrounding the inner opening act independently of the cells in the other rings. As a definite example of a species with pores that can be closed he quotes *M. nitida* Lehm. & Lindenb., a species which is to be regarded as a synonym of *M. paleacea.*

[23] Rabenhorst's Kryptogamen-Flora 6: *f. 188.* 1907.
[24] Flora 84 (Ergänzangsb.): 46. 1897.

2. Compact Ventral Tissue

The ventral tissue in *Marchantia* gradually thins out from the thickened median portion until it is frequently only two or three cells thick along the margins of the thallus. It consists primarily or even wholly of parenchyma and its chief function apparently is to act as a storage-tissue for water and organic food. In some parts of the thallus it is usually possible to demonstrate the presence of elongated pits in the cell-walls, and a purplish pigmentation of the walls is often apparent. Cells containing oil-bodies are usually conspicuous among the other parenchyma cells (Fig. 20, A) and seem to be present in all the species. In herbarium material, however, it is not always easy to demonstrate them. Cells containing mycorrhiza are likewise very frequent. In *M. chenopoda,* as noted by Leitgeb and Prescher, the ventral tissue and the partition walls between the air-chambers contain scattered slime-cells similar to those found in the epidermis. Slime-cells of this character occur also in the compact tissue of *M. paleacea, M. breviloba* sp. nov. and the East Indian *M. emarginata,* but have not yet been detected in other species except in connection with the reproductive organs. According to Cavers[25] the slime-cells and slime-canals of *Conocephalum conicum* fail to develop when the plants are cultivated under water, and it is therefore possible that slime-cells may not always be present in the species of *Marchantia* just listed. In fact Prescher reported that they were absent from *M. emarginata,* and specimens of *M. paleacea* and of *M. chenopoda* might be cited where they are very infrequent or perhaps not present at all.

The only cells found in the ventral layer which are not parenchymatous in their nature are the more or less elongated sclerotic cells with yellow or brown walls, which occur in certain species. Cells of this character were first demonstrated by Goebel[26] in the case of *Preissia quadrata* (Scop.) Nees, and the same author has called attention to their occurrence in the New Zealand *M. foliacea* Mitt.[27] In this species, according to his account, the sclerotic cells are variable in length and are usually scattered singly among the parenchyma cells. Occasionally two

[25] Ann. Bot. **18**: 93. 1904.
[26] Arb. Bot. Inst. Würzburg **2**: 533. 1882.
[27] Flora **96**: 194. *f. 143.* 1906.

cells will occur end to end and sometimes even longer groups or strands are formed, perhaps corresponding with Stephani's "strands of sclerenchyma." The walls of the cells are thick and pigmented, showing that their functions are primarily mechanical, but Goebel finds that the cavities sometimes contain starch-grains. Sclerotic cells occur in several American species, such as *M. paleacea, M. chenopoda* (FIG. 20, A, B) and *M. domingensis,* and agree closely with Goebel's description. Whether they are always produced by the species where they have been detected is perhaps a question. Cavers[28] calls attention to the fact that *Preissia quadrata,* when grown indoors in a moist atmosphere, fails to develop thick-walled cells, and in all probability the formation of the similar cells in *Marchantia* is influenced by environmental conditions. In any case, however, the presence of sclerotic cells is associated with certain definite species.

3. VENTRAL SCALES

The ventral scales in *Marchantia* exhibit considerable diversity, not only when different species are compared but also when an individual species is considered. This is due to the fact that each species produces at least two distinct kinds of scales, only one of which bears appendages. In the other genera of the Marchantiaceae the scales with appendages are the only kind produced.

Taylor[29] was apparently the first to observe that the scales in *M. polymorpha* were not all alike. He distinguished three different kinds, and these are described at length by Leitgeb,[30] who designates them as median, laminar and marginal scales, respectively. The median scales are attached by a long line, which begins near the axis of the thallus, then extends almost longitudinally and finally curves gently outward, reaching perhaps half way to the margin. The scales are at first very narrow but become abruptly dilated in the outer part; here on each scale the characteristic appendage is attached, strongly contracted at its junction with the scale and then abruptly dilated into an orbicular expansion, rounded to apiculate at the apex (FIG. 1).

[28] Contrib. to the Biol. of the Hepat. 28. Leeds and London, 1904.
[29] Trans. Linn. Soc. 17:377. 1835.
[30] Unters. über Leberm. 6: 114. 1881.

The laminar scales are more numerous than the median scales and form a series about midway between the median scales and the margin. They are attached by a much shorter line and broaden out at once into lunulate or ovate structures, rounded at the apex and destitute of appendages. The marginal scales are still more numerous and attached by even shorter lines, but they resemble the laminar scales in lacking appendages and in most other respects. They are situated near the margin and some of them extend beyond. The arrangement of the scales is shown clearly in a figure by Goebel,[31] who brings out the fact that the laminar scales are arranged in an irregular row and that the marginal scales are still more irregular in their arrangement, although a linear series is approximated.

The account of the scales just given is somewhat at variance with the description and figures of Müller.[32] According to this author the innermost scales are long and very narrow; they are attached almost longitudinally throughout their entire length and are destitute of appendages. These are said to be borne instead on the scales of the next outer row, which agree in all respects with the median scales as described by Leitgeb. The third type of scale recognized by Müller includes both the laminar and marginal scales of Leitgeb. An interpretation of the scales, closely agreeing with Müller's, has recently been published by Massalongo.[33] The present writer, however, has been unable to demonstrate the narrow innermost scales without appendages. According to his observations the statements of Leitgeb are essentially correct.

The scales in *M. polymorpha,* as well as in the other species, are delicate in texture and are sometimes more or less pigmented; in most cases, however, the pigmentation is of short duration and the scales become bleached and transparent. The cells tend to be wavy and irregular, especially toward the margin (Figs. 7, A; 20, C). The cell-walls are thin, although trigones may sometimes be demonstrated on the marginal scales. Scattered about among the other cells are cells containing oil-bodies (Fig. 20, D) and rhizoid initials, the latter giving rise to tuberculate rhizoids (Fig. 20, E). In the appendages rhizoid initials are absent, but cells containing oil-bodies can often be distinguished (Figs. 1, 3, etc.).

[31] Organographie der Pflanzen *f. 158.* Jena, 1898.

[32] Rabenhorst's Kryptogamen-Flora 6:17. *f. 12.* 1905.

[33] Atti R. Ist. Veneto 75:696. *pl. 4, f. 12-15.* 1916.

According to Leitgeb the scales in certain species, such as *M. domingensis* and *M. nitida,* are all of the median type while in *M. chenopoda* the laminar scales are less numerous than the median scales and the marginal scales are absent altogether. In Goebel's figure of *M. chenopoda*[84] a single laminar scale is shown among sixteen median scales and the implication is made that the number of laminar scales is very small. The writer has examined numerous specimens of *M. paleacea* (which includes *M. nitida*), of *M. chenopoda* and of other species and finds laminar scales always present (see Fig. 6, H-O). They differ from the laminar scales in *M. polymorpha,* however, in being situated much closer to the median scales. On account of their shorter lines of attachment they extend only a small part of the distance toward the median line. The laminar scales usually alternate with the median scales but occasionally there may be two laminar scales between two successive median scales. Under these circumstances one of the laminar scales is often reduced in size.

The species just noted will give some idea of the differences in arrangement which the ventral scales may show. These differences can often be utilized in separating species, but the best differential characters yielded by the scales are those drawn from the appendages. These are, with very rare exceptions, borne singly and, as has been shown, are confined to the median scales. Although the appendages vary, within wide limits in certain species, they nevertheless present striking and distinctive features. In comparing them the form, the character of the margin and apex, the size of the cells, and the presence or absence of cells containing oil-bodies should be taken into consideration. With respect to size the cells may be approximately the same throughout the entire extent of an appendage (see Fig. 16, F, G). It is much more usual, however, for the median cells to be much larger than the marginal cells and the gradation from one to the other may be either gradual (see Fig. 7) or very abrupt (see Fig. 5, A-D). The texture of the scales, aside from the appendages, is much the same throughout the genus. The scales and their appendages will be again considered in connection with the various species discussed below.

[84] *L. c. f. 157.*

4. Rhizoids

The rhizoids in the genus *Marchantia,* as in practically all of the Marchantiales, are of two types, the smooth and the tuberculate. In the smooth type the walls are thin or uniformly thickened; in the tuberculate type numerous local thickenings of the wall extend into the lumen of the rhizoid in the form of cylindrical or bluntly conical projections. In some of the tuberculate rhizoids the projections are discrete and irregular in their distribution; in others they are more or less coalescent and show a spiral arrangement. Kamerling[35] has shown that these spiral tuberculate rhizoids are abundant in *M. polymorpha* and Schiffner[36] has examined this and other species of the genus with reference to these peculiar structures. He confirms Kamerling's statements about their occurrence in *M. polymorpha* and finds, so far as American species are concerned, that they are equally abundant and typical in *M. chenopoda;* that they still occur, although in less typical form, in *M. domingensis* and its allies; and they are wanting altogether in *M. paleacea.*

Most of the rhizoids in *Marchantia* run in parallel bundles under the scales and converge to form a single large median bundle. There are, however, numerous rhizoids in the thickened median portion which spread at right angles to the surface, and Schiffner has made a number of interesting observations on these. In forms of *M. polymorpha* where a definite dorsal band lacks air-chambers, the rhizoids in question are smooth; in forms where the air-chambers extend across the median region, the rhizoids are tuberculate. In *M. plicata* the spreading rhizoids are smooth; in *M. chenopoda,* smooth; in *M. Berteroana,* tuberculate; in *M. paleacea,* smooth or with scattered tubercles. These differences may sometimes be of help in distinguishing species.

5. Receptacles

The receptacles in *Marchantia* are strikingly different from the vegetative branches and attain a higher degree of complexity than in any other genus of the group. Two distinct portions may be distinguished, the erect stalk and the horizontal disc (or recep-

[35] Flora 84 (Ergänzungsb.) : 31. *pl. 1, 2, f. 7.* 1897.

[36] Ann. Jard. Bot. Buitenzorg 2 (Suppl. 3) : 489, 490. 1909.

tacle proper), which bears the sexual organs. In some cases the disc shows clearly that it has but one plane of symmetry. In other cases it presents the appearance of being radial; but even here, as recently emphasized by Goebel,[37] there is actually but a single plane of symmetry, a fact made clearly evident when the structure and development of the receptacle are considered. The stalk, likewise, looks superficially as if it were radial, but here again a single plane of symmetry is present, and the stalk maintains its dorsiventrality (or zygomorphy) in spite of its erect position.

It has already been noted that the receptacles represent prolongations of prostrate branches. These branches may be more or less elongated, but they are often very short, a receptacle being developed almost immediately after a dichotomy has taken place. A receptacle, as shown so clearly by Leitgeb,[38] is a branch-system, the growing point of the original prostrate branch undergoing one or more divisions. A study of the stalk shows that the first division usually takes place very early in the development of the receptacle. If a cross-section is examined (Figs. 5, K; 8, 5; etc.) the dorsiventrality of the stalk becomes at once apparent, and the side which represents the ventral portion usually shows two deep longitudinal furrows, enclosed by scales and containing tuberculate rhizoids, the dorsal side being destitute of such furrows. In very rare cases a single furrow is present near the base of the stalk (Fig. 20, I). The presence of two furrows is evidence that the growing point has already divided once, even if the stalk itself remains undivided. Usually no further divisions take place until the disc begins to develop, but in some cases the stalk shows three or four rhizoid furrows, indicating that one or two secondary divisions have occurred. This is seen clearly in *M. breviloba* and *M. domingensis* (Figs. 9, I-K; 12, A, D). In the first the stalks of both male and female receptacles show four furrows apiece; in the second the stalk of the male receptacle which is figured shows three furrows, the stalk of the female receptacle showing four. The occurrence of more than two furrows has apparently been rarely observed in *Marchantia* and allied

[37] Organographie der Pflanzen, 2d ed. 686. 1915.
[38] See Unters. über Leberm. 6: 20-37. 1881.

genera. Spruce[39] mentions the occasional presence of three furrows in the stalk of the female receptacle in *Marchantia,* without citing definite species; Leitgeb,[40] in a single instance, found four furrows in the stalk of the female receptacle in *Preissia quadrata;* Stephani[41] states that the stalk of the male receptacle in the African *M. Wilmsii* Steph. has four furrows but doubts the constancy of this condition; and Schiffner[42] notes that the stalk of the female receptacle in *Bucegia romanica* Radian sometimes shows four furrows. These seem to be the only references to more than two furrows in the literature, but in all probability a higher number than two would occasionally be found in most species of *Marchantia* if enough stalks were examined. In *M. breviloba* four furrows seem to be the rule in the female receptacle, although it would hardly be safe to state that four were always present.

In the case of *M. polymorpha* it was noted long ago by Mirbel that the dorsal side of the stalk of the female receptacle showed a distinct strip of photosynthetic tissue with air-chambers, epidermal pores and short green filaments. This strip seems to be of constant occurrence throughout the genus. It commences close to the base of the stalk and extends nearly to the disc. In most cases the strip is continuous (Figs. 5, K; 8, J; 9, K; etc.) but sometimes, as in *M. chenopoda,* it may be separated into two strips by a median groove (Fig. 20, G-I). In the stalk of the male receptacle photosynthetic tissue is usually absent, the dorsal portion being composed of compact parenchyma. In certain species, however, such as *M. domingensis,* the photosynthetic tissue is about as well developed in the male (Fig. 12, A) as in the female receptacle. In *M. breviloba* the lower part (Fig. 9, I) of the stalk develops photosynthetic tissue while the upper part (Fig. 9, J) lacks it completely.

In the disc of the male receptacle the dichotomous branching usually continues and a distinct division into rays becomes apparent. Although the number of rays is subject to variation, certain numbers seem to be normal or typical for certain species. In *M. polymorpha,* for example, there are usually eight rays

[39] Trans. Bot. Soc. Edinburgh **15**: 558. 1885.
[40] Unters. über Leberm. **6**: 31. 1881.
[41] Hedwigia **31**: 196. 1892.
[42] Beih. Bot. Centralbl. **23**^{2}: 282. *f. 16.* 1908.

present and in *M. chenopoda,* four, although deviations from these numbers are of frequent occurrence. Goebel[43] considers that the number of rays developed is dependent on nutritive conditions. In an unnamed species from the Fiji Islands, related to *M. geminata,* he notes a reduction in the number of rays to two, showing that only one dichotomy has taken place, and he compares this extreme condition with the two-rayed female receptacles found in *Exormotheca* and *Aitchisoniella.*

The rays are in one plane and vary greatly in length. They are sometimes much shorter than the undivided portion of the receptacle, appearing in the form of rounded marginal scallops separated by shallow but acute sinuses. This condition is seen clearly in *M. polymorpha* and its allies. It is much more usual, however, for the rays to be longer than the undivided portion, the whole receptacle thereby acquiring a palmate appearance. This type of receptacle is found in such species as *M. chenopoda* and *M. domingensis* and is commonly associated with a smaller number of rays than the first type. In some cases at the tip of a ray a slight depression marking the position of a growing point can be discerned, even in an old receptacle, but often all traces of the growing points disappear. The stalk is not attached to the disc marginally but peltately, although often excentrically. The peltate attachment is due to intercalary growth taking place in the region where the dorsal surface of the stalk and the dorsal surface of the disc would naturally be continuous. In this way a thin plate of tissue is formed between the two external rays of the disc, which would theoretically be distinct to their junction with the stalk. The presence of this plate, similar in all essential respects to the tissue forming the sinuses, intensifies the radial appearance which the receptacles of certain species show.

In its structure the disc shows many of the features which are found in the vegetative thallus. It is distinctly dorsiventral and the differentiation into epidermis, photosynthetic tissue and compact ventral tissue is clearly marked. On the ventral surface of the rays scales with appendages and scales without appendages can be distinguished in two or more series, and the appendages are much like those of the ordinary scales except that they are smaller and sometimes less constricted at the base. Rhizoid

[43] Organographie der Pflanzen, 2d ed. 699. *f. 669 II.* 1915.

initials are present among the cells of the scales, the appendages alone being free from them.

The antheridia arise in acropetal succession, the oldest being formed near the center of the disc. In many species each ray develops two distinct rows of antheridia, but in certain species, such as *M. polymorpha,* the antheridia are more irregular in their arrangement and each ray shows more than two indistinct rows. The antheridia are borne singly in deep depressions with small circular openings. The depressions extend down into the compact ventral tissue, and are surrounded by the characteristic air-spaces with their branched rows of photosynthetic cells and dolioform epidermal pores.

The stalk of the female receptacle develops more slowly than that of the male receptacle and persists in an active condition until the sporophytes are mature. In the disc the division into rays takes place just as in the male receptacle and the number of rays present is subject to similar variations. The archegonia form groups and arise in acropetal succession, beginning when the disc is very young; but, on account of the strong intercalary growth in the median region of the dorsal portion, the archegonia are arched over and displaced until they seem to be situated on the ventral surface of the disc. In this way the oldest archegonia come to lie nearest the periphery of the disc and the youngest nearest the stalk. Each group of archegonia contains a variable number, arranged in two or three more or less definite radial rows, and is derived from one of the growing regions of the disc.

In the East Indian *M. geminata* and its allies the groups of archegonia are clearly situated underneath the rays of the receptacle. These rays, therefore, are obviously homologous with the rays of the male receptacles throughout the genus. This condition, however, is very exceptional. In most species of the genus, including all the American representatives, the groups of archegonia alternate with the rays of the receptacle and are situated in the sinuses between them. This is caused by the rapid intercalary growth of the regions between the growing points, the so-called "middle lobes"; the rays, accordingly, are formed by the middle lobes and are not homologous with the rays of the male receptacle but rather with the sinuses. These relationships are discussed at length by Leit-

geb,[44] who notes also the fact that the two external rays are to be compared with the "side lobes" in an ordinary dichotomy. In *M. polymorpha,* where nine rays are commonly present, seven would represent middle lobes and two, side lobes. Between the two side lobes there is of course no group of archegonia, so that there are eight groups for the entire receptacle, showing that three dichotomies have taken place.

The rays of the female receptacles vary in length, very much as in the case of the male receptacles. There is, however, no correspondence between the two. In *M. polymorpha,* for example, the rays of the female receptacle are long, and those of the male receptacle are short, while in *M. chenopoda* the conditions are reversed. The rays of the female receptacle differ also in form, being flat in some species and cylindrical in others. When they are flat they are often retuse or shortly bilobed at the apex, and Goebel points out that a deepening of the apical sinuses would lead to the condition found in *M. geminata,* where sinuses instead of rays are present between the groups of archegonia. In young receptacles the rays are strongly curved downward, but they gradually straighten out if fertilization has taken place and assume a horizontal position.

On account of the strong intercalary growth which displaces the archegonia to the lower surface of the disc, the portion of the receptacle which is morphologically ventral is less extensive than at first appears. The lower surface between the groups of archegonia is ventral in character and the same thing is of course true of the lower surface of the rays, especially when these represent the middle lobes of the branch-system. Even here, however, when the rays become cylindrical through intercalary dorsal growth, the ventral surface is much less extensive than the dorsal. In *M. geminata* the ventral surface of the rays is situated on both sides of the groups of archegonia. The ventral surface is characterized by the presence of tuberculate rhizoids and slender scales, the latter being sometimes branched and strikingly different from the ventral scales of the vegetative thallus. The dorsal portion (except where the archegonia are situated) develops a complex system of air-chambers of the usual type.

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[44] Unters. über Leberm. 6 : 34. 1881.

Each group of archegonia is enclosed by an involucre, which consists of a pair of membranous structures often toothed or laciniated on the margin (Figs. 2, M; 4, F, G; 8, K; etc.). Each archegonium is further protected by a campanulate pseudoperianth contracted at the mouth to a small opening. It begins its development soon after the archegonium is formed but does not reach full maturity unless fertilization has taken place. The pseudoperianth is very delicate and becomes irregularly torn when the stalk of the sporophyte elongates.

6. Sporophyte

The sporophyte, as in all the Marchantiaceae, shows the usual differentiation into foot, stalk and capsule. The foot is flattened and forms a low ridge enclosing the base of the stalk. The latter is at first very short, but it elongates sufficiently at maturity to push the capsule through the calyptra and beyond the mouth of the pseudoperianth. The capsule constitutes the principal part of the sporophyte. It is nearly spherical in form and is bounded on the outside by a wall composed of a single layer of cells. These cells throughout the genus have brownish ring-like thickenings in their walls, although the rings are often incomplete. The entire cavity of the capsule is filled with spores and elaters. The spores are much smaller than in most genera of the Marchantiaceae, especially in *M. polymorpha* and its allies. In some cases a distinct border is present where the spherical face meets the three plane faces, and under these circumstances low and irregular surface lamellae are usually developed. In other cases the spores are destitute of distinct markings and become completely rounded off after the tetrads break up. The elaters are long and slender and of the usual type, showing two distinct spiral bands. At maturity the wall of the capsule splits from the apex to about the middle into an indefinite number of lobes, some of which may become further subdivided. There are apparently no very definite lines of dehiscence, the edges of the splits being irregular and jagged from projecting cells which formerly interlocked. Except for the spores, which differ in size and in the peculiarities of their walls, the sporophyte yields very few differential characters.

7. Cupules

The characteristic gemmae of *Marchantia* have been repeatedly described. They consist of flat discoid structures, each bearing two opposite marginal growing points in shallow indentations. They are attached to the thallus by a short stalk, which joins the margin of the gemma midway between the growing points, the gemma in consequence being vertical in position. The gemmae occur in clusters on the upper surface of the thallus and are surrounded by a circular membranous outgrowth, forming a cup or cupule. Although the gemmae are very uniform throughout the genus, the cupules yield a few differences which sometimes assist in the determination of species. Two principal types occur: in the one, the margin of the cupule is simply dentate to ciliate, the teeth being sometimes scattered and sometimes close together; in the other type the margin bears a series of triangular pointed lobes, the edges of which are dentate to ciliate. As an example of the first type *M. domingensis* (Fig. 12, K) may be cited, while *M. polymorpha* (Fig. 2, N) shows the second type clearly.

III. DESCRIPTION OF SPECIES

Nees von Esenbeck[1] divided the genus *Marchantia* into the two sections *Astromarchantia* and *Chlamidium*. The first included species in which the female peduncle was "central"; the second, which was first proposed by Corda as a genus, included species in which the female receptacle was "excentric." In the first section he placed *M. polymorpha,* in the second *M. paleacea.* These two sections are retained in the Synopsis Hepaticarum, except that the first is renamed *Stellatae;* they are likewise retained by Dumortier,[2] who coined the name *Marchantiotypus* for the first section. Schiffner[3] follows the example of the Synopsis, emphasizing the radial symmetry of the female receptacle in the *Stellatae;* while Stephani bases his two groups, "a" and "b," which he does not designate by formal names, upon differences in the symmetry of the female receptacle, the first group including species with "symmetrical" receptacles and the second, species with "unsymmetrical" receptacles. It is interesting to note that he includes *M. paleacea* in his first group, although his predecessors had placed it definitely in the section *Chlamidium.*

The fact has already been brought out that the female receptacles throughout the genus are always symmetrical with respect to one plane of symmetry but never with respect to more than one. Stephani's distinction, therefore, falls to the ground, and the distinction in the position of the stalk, emphasized by Nees von Esenbeck, is not much more trustworthy. In certain species, where the two basal rays are sometimes distinctly shorter than the others and sometimes about as long, it breaks down altogether; in the first case the stalk would be "excentric," in the second "central." At the same time the sections *Astromarchantia* and *Chlamidium* represent natural groups of species and can still be maintained if different characters are used to distinguish them. In *Astromarchantia,* for example, there are no sclerotic cells in the thallus, and the rays of the female receptacle are terete, at least in the outer part; in *Chlamidium,* sclerotic cells

[1] Naturg. Europ. Leberm. 4: 60. 1838.
[2] Bull. Soc. Bot. Belgique 13: 150. 1874.
[3] Engler & Prantl, Nat. Pflanzenfam 1^3: 37. 1893.

are normally present in the thallus, and the rays of the female receptacle are flat or convex. In both these sections the involucres (and clusters of archegonia) alternate with the rays. A third group, typified by *M. geminata,* in which the involucres are situated beneath the rays, also seems worthy of sectional rank, but since this group is not represented in America (at any rate according to our present knowledge), it need not be further considered here.

In the preparation of this paper the writer has had the privilege of examining the large collection of *Marchantiae* in the herbarium of the New York Botanical Garden (N. Y.),[4] which includes the Mitten and Underwood herbaria. This has been supplemented by the specimens in the Cryptogamic Herbarium of Harvard University (H.), which includes the Taylor and Sullivant herbaria, and by the material in the United States National Herbarium (U. S.), the private herbarium of Miss C. C. Haynes (C. C. H.), and the herbaria at Yale University (Y.), the last including the Eaton herbarium and the writer's private herbarium. Several specimens from the Montagne (M.) and Boissier (B.) herbaria, including a number of types, have likewise been available for study, through the courtesy of MM. Paul Hariot and G. Beauverd, respectively. The writer would extend his sincere thanks to all who have aided him in his work.

Key to the species

Thallus destitute of sclerotic cells: stalk of male receptacle destitute of air-chambers, with two rhizoid-furrows; rays short and broad: stalk of female receptacle with a single band of air-chambers and two rhizoid-furrows; rays mostly nine or more, terete, at least in outer part; involucre with dentate or ciliate lobes: cupules with dentate lobes, bearing papillae on outside.

Section I. Astromarchantia.

Epidermal pores usually surrounded by four rows of cells, never distinctly cruciate: marginal scales present; appendages of median scales irregularly crenulate or denticulate.

Rays of female receptacle bearing papillae; basal sinus scarcely or not at all wider than the others.

1. *M. polymorpha.*

Rays of female receptacle destitute of papillae; basal sinus usually distinctly wider than the others.

2. *M. plicata.*

[4] The letters in parentheses are abbreviations used below in the citation of specimens.

Epidermal pores usually surrounded by six rows of cells, distinctly cruciate; marginal scales not present; appendages of median scales minutely and regularly crenulate or denticulate; rays of female receptacle destitute of papillae; basal sinus scarcely or not at all wider than the others.

3. *M. Berteroana.*

Thallus with sclerotic cells: epidermal pores usually surrounded by five to seven rows of cells: marginal scales not present: rays of female receptacle mostly five to nine, rarely more, flat to convex on upper surface, never terete, destitute of papillae; basal sinus usually distinctly wider than the others: cupules destitute of papillae.

Section II. Chlamidium.

Stalk of female receptacle with a single band of air-chambers.

Epidermal pores cruciate: appendages of scales entire or slightly toothed: stalk of male receptacle destitute of air-chambers, with two rhizoid-furrows; rays short and broad: stalk of female receptacle with two rhizoid-furrows; rays long and narrow; involucre with ciliate lobes: cupules with dentate lobes.

4. *M. paleacea.*

Epidermal pores not cruciate: stalk of male receptacle with a single band of air-chambers and two to four rhizoid-furrows; rays long and narrow (at maturity): stalk of female receptacle with two to four rhizoid-furrows; involucre vaguely or not at all lobed, entire to ciliate: cupules not lobed, dentate to ciliate.

Appendages of ventral scales sparingly crenulate or denticulate: rays of female receptacle short and broad, mostly eleven; involucre ciliate.

5. *M. breviloba.*

Appendages of ventral scales usually closely denticulate or ciliolate: rays of female receptacle long and usually narrow.

Epidermal pores mostly 90-130 x 70-80μ: rays of female receptacle slightly or not at all dilated at the apex, rarely emarginate; involucre crenulate to ciliate.

6. *M. domingensis.*

Epidermal pores mostly 50-70 x 40-45μ: rays of female receptacle distinctly dilated at the apex, usually emarginate; involucre entire to crenulate.

7. *M. papillata.*

Stalk of female receptacle with two bands of air-chambers and two rhizoid-furrows; rays normally five, short and rounded, not dilated; involucre dentate to ciliate or laciniate: stalk of male receptacle with two rhizoid-furrows: epidermal pores not cruciate: appendages of ventral scales entire to sparingly dentate: cupules not lobed, dentate to ciliate.

Thallus thin and very delicate.

8. *M. Bescherellei.*

Thallus usually thick and firm.

9. *M. chenopoda.*

Section I. **Astromarchantia**

1. Marchantia polymorpha L.

Marchantia polymorpha L. Sp. Plant. 1603. 1753.
Marchantia stellata Scop. Fl. Carn. 24 ed. 353. 1772.
Marchantia umbellata Scop. *l. c.* 354. 1772.
Marchantia coarctata Corda; Opiz, Beitr. zur Naturg. 647. 1828 (*nomen nudum*).
Marchantia elliptica Corda, *l. c.* 647. 1828 (*nomen nudum*).
Marchantia Kablichiana Corda, *l. c.* 647. 1828 (*nomen nudum*).
Marchantia macrocephala Corda, *l. c.* 647. 1828. (*nomen nudum*); Sturm, Deutschl. Flora 2:63. *pl. 17.* 1832.
Marchantia vittata Raddi, Mem. Soc. Ital. Modena 20:45. 1829.
Marchantia Syckorae Corda; Nees von Esenbeck, Naturg. Europ. Leberm. 4:97. 1838.
Marchantia oregonensis Steph.; Röll, Bot. Centralbl. 43:203. 1891.

Thallus pale to dark green, not glaucous, sometimes with a brownish or purplish median band on the upper surface, often more or less pigmented with purple on the lower surface, usually 0.75-1.25 cm. wide and 4-6 cm. long, repeatedly dichotomous, the successive forks usually 2 cm. or less apart; texture sometimes delicate, sometimes firm, but never leathery, margin entire or minutely denticulate; epidermis composed of cells with thin or slightly thickened walls, mostly 20-60μ long (averaging about 29μ) and 12-20μ wide (averaging about 16μ), papillae present near the margin or absent altogether; pores (with their surrounding cells) mostly 60-75μ long and 40-60μ wide, sometimes measuring as much as 90 x 65μ, surrounded usually by four rows of cells (two in each series), each row being usually composed of four cells, inner opening usually four-sided, the sides rarely concave throughout, each bounding cell usually projecting inward in the form of a rounded papilla with subparallel or converging sides, mostly with a resinous deposit; air-chambers low, more or less elongated, their boundaries indistinct when viewed through the epidermis, usually present everywhere (except close to the margin) but sometimes absent from the median region, rows of photosynthetic cells sometimes three cells long but often shorter; compact ventral tissue mostly twelve to twenty cells thick in the median portion, destitute of slime cells and sclerotic cells, the cell walls slightly thickened and showing distinct pits; ventral scales in three rows on each side of the thallus, median and marginal scales in distinct rows, laminar scales in a more indefinite row, scales often more or less pigmented

with purple, the marginal scales close together though scarcely imbricated, usually projecting beyond the margin; appendages of median scales broadly orbicular, mostly 0.5-0.75 mm. long and 0.6-0.8 mm. wide, rounded to very bluntly pointed, sometimes apiculate, margin usually minutely and irregularly denticulate, sometimes (in hygrophilous forms) tending to be crenulate, cells showing a gradual decrease in size toward the margin, median cells subisodiametric, mostly 35-40μ in diameter, marginal cells mostly 20-25μ long and 14-16μ wide, sometimes smaller (10-16μ x 10μ), cells containing oil-bodies about 20μ in diameter, usually from five to ten on each appendage, restricted to submarginal (and, rarely, marginal) portions: male receptacle borne on a stalk 1-3 cm. long with two rhizoid-furrows, destitute of dorsal air-chambers, the disc mostly 0.7-1 cm. broad, shortly lobed or merely crenate, the lobes or rays mostly eight (rarely nine or ten), 2 mm. long or less, rounded at the apex with thin wavy margins, covered ventrally with densely imbricated scales in several rows: female receptacle borne on a stalk 2-7 cm. long, with two rhizoid-furrows and a single broad dorsal band of air-chambers, the disc mostly 0.8-1.3 cm. broad, deeply lobed, the lobes or rays spreading at maturity, mostly nine (sometimes ten or eleven), 3-5 mm. long, separated by subequal sinuses, terete, covered over with epidermal papillae; involucre deeply and irregularly lobed, the lobes long-acuminate and ciliate on the margins: spores yellow, 12-15μ in diameter, nearly smooth; elaters 3-5μ wide, bispiral: cupules deeply lobed, the lobes acute to acuminate, usually dentate to short-spinose on the sides, outer surface with epidermal papillae. (Figs. 1, 2.)

Throughout the greater part of Europe and in the northern parts of Asia and North America *M. polymorpha* is the only representative of the genus and is exceedingly abundant. It grows in swamps and bogs, on rocks and walls near the ground, on banks and the sides of ditches, in gardens and greenhouses, and on the earth in fields and woods. It is perhaps most luxuriant in bogs and on steep rocky hillsides where a liberal supply of water is available. In the woods it is especially likely to occur where a fire has left a supply of charcoal behind. Toward the south other species of *Marchantia* make their appearance and *M. polymorpha* becomes less abundant. In many places it presents the appearance of being an introduced plant.

A search through the literature shows that the occurrence of *M. polymorpha* south of the equator has been doubted or denied by certain authors. Hooker,[5] for example, about fifty years ago,

[5] See Handb. New Zealand Fl. 545. 1867.

stated that *M. tabularis* (i. e., *M. Berteroana*) was the southern representative of the northern *M. polymorpha,* thus implying that the latter species was absent from antarctic regions. Stephani[6] is even more definite when he describes the habitat of the species as "Europa, Asia et America septentrionalis." Other authors, however, cite definite stations for *M. polymorpha* from the Southern Hemisphere. It will be sufficient to mention in this connection the recent record by Schiffner[7] for Kerguelen Island, that by Kaalaas[8] for the Crozet Islands, and that by Howe[9] for South Georgia. In the opinion of the present writer the occurrence of the species in South America has been clearly established. Specimens from Ecuador, Bolivia and Patagonia have been carefully studied and have been found to agree in all essential respects with European and North American material. Specimens from Kerguelen Island, collected by the Challenger Expedition, and the specimens from South Georgia cited above have likewise been examined, and have been found equally convincing, but no further statements can be made from personal knowledge regarding the distribution of the species in other parts of the Southern Hemisphere.

On account of the abundance of *M. polymorpha* in the United States and northward it seems inadvisable to give a full list of the North American specimens which have been examined. It is enough to state that the species has been collected in Greenland and other parts of arctic America, in Alaska, in nearly every Canadian province and territory and in nearly every state of the Union. The specimens cited below are from tropical North America and from South America.

Federal District of Mexico: Cañada San Magdalena, Contreras, October, 1908, *Barnes & Land 455, 458* (Y.).

Oaxaca: near Miahuatlan, 1895, *E. W. Nelson 2530* (U. S.).

Puebla: banks along Avenida Hidalgo and path to barranca, Tezuitlan, October, 1908, *Barnes & Land 541, 542* (Y.); Santa Barbara, near Puebla, November, 1909, *Frère Nicolas 20* (Y.).

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[6] Bull. Herb. Boissier 7: 393. 1899.

[7] Deutsch. Südpolar-Exped. 8: 64. 1906.

[8] Nyt Mag. Naturv. 49: 86. 1911.

[9] See Taylor, N. Sci. Bull. Mus. Brooklyn 2: 62. 1914.

Vera Cruz: Orizaba, 1855, *F. Müller 2245* (N. Y., listed by Gottsche in Mex. Leverm. 268. 1863); Mirador, April, 1857, *C. Mohr* (N. Y.); Orizaba, January, 1892, *J. G. Smith* (N. Y.).

Jamaica: near Hardware Gap, July, 1903, *A. W. Evans 176* (Y.).

Ecuador: near Baños, *R. Spruce* (distributed in Hepaticae Spruceanae).

Bolivia: Sorata, February, 1886, *H. H. Rusby 3005* in part (N. Y., listed by Spruce as *"M.* nova species?" in Mem. Torrey Club 1: 140. 1890).

Chile: Renca, near Santiago, February, 1901, *G. T. Hastings 318* (U. S.); Straits of Magellan, 1866-67, *A. Cunningham 105, 135* (N. Y.); Punta Arenas, November, 1895, *P. Dusén* (N. Y., first determined by Stephani as *M. Berteroana;* afterwards listed as *"M. tabularis"* in Bihang t. K. Sven. Vet.-Akad. Handl. 26^3, No. 17: 8. 1901); Cordilleras of Patagonia, February, 1897, *J. B. Hatcher* (Y., listed by the writer in Bull. Torrey Club 25: 424. 1898); Punta Arenas, February, 1906, *R. Thaxter* 64, 65 (H., Y.).

The following additional stations, recorded in the literature, are likewise of interest:

Costa Rica: Volcano of Poas, *H. Pittier 6021* (listed by Stephani in Bull. Soc. Bot. Belgique 31: 180. 1892).

Colombia: Bogota, 1859, *A. Lindig 1700, 1701, 1717* (listed by Gottsche in Ann. Sci. Nat. Bot. V. 1: 186. 1864).

Venezuela: Colonia Tovar, *Moritz 134* (listed, but erroneously ascribed to Colombia, in Syn. Hep. 789. 1847; also listed by Hampe in Linnaea 20: 333. 1847).

Ecuador: Tunguragua, *R. Spruce* (listed in Trans. Bot. Soc. Edinburgh 15: 560. 1885).

As its name implies, *Marchantia polymorpha* is an exceedingly variable species, and a full account of its numerous forms is given by Nees von Esenbeck.[10] He recognizes two principal varieties, A. *Communis* and B. *Alpestris,* and under each variety he describes a series of sub-varieties and groups of more inferior rank. A. *communis* is prevalent at lower altitudes but sometimes ascends to higher elevations in sheltered localities; B. *alpestris* is restricted to mountainous regions. A. *communis* is charac-

[10] Naturg. Europ. Leberm. 4: 65-71. 1838.

terized by a lax habit and by female receptacles having elongated rays and long slender stalks; B. *alpestris,* by a compact habit and by female receptacles having shorter rays and shorter and thicker stalks.

Nees von Esenbeck's varieties and subordinate groups are accepted without question in the Synopsis Hepaticarum, but later

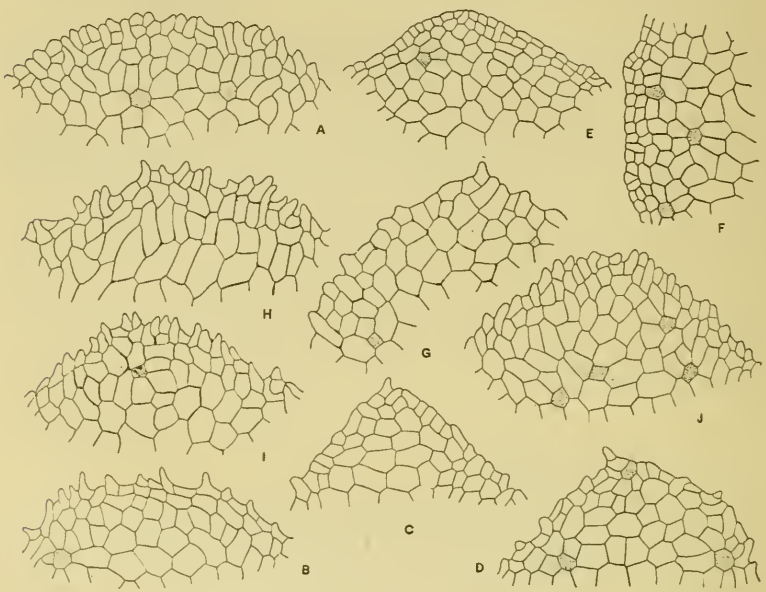

FIG. 1. MARCHANTIA POLYMORPHA L.

Appendages of ventral scales, x 100; F represents the basal portion of an appendage; the other figures represent apical portions. A. Opdal, Norway, *J. Hagen,* in V. Schiffner's Hep. Europ. Exsic. *15,* type of var. *mamillata* Hagen. B-D. New Haven, Connecticut, *A. W. Evans.* E, F. Wilbraham, Massachusetts, *E. A. Chapin,* forma *aquatica.* G. Mount Hood, Oregon, *J. Röll,* type of *M. oregonensis* Steph. H. Oaxaca, *E. W. Nelson 2530.* I. Jamaica, *A. W. Evans 176.* J. Patagonia, *J. B. Hatcher.*

writers have largely neglected them. There are two, however, which appear from time to time in local lists and taxonomic works. One of these is A. *communis, α aquatica,* usually quoted as "var. *aquatica* Nees," and the other is B. *alpestris,* quoted as "var. *alpestris* Nees." The differences between these two so-called varieties are indeed striking. In var. *aquatica* the thallus shows a distinct median band on the upper surface usually pigmented with purple and associated with the absence of air-

chambers, as Schiffner has pointed out; in var. *alpestris* the thallus is uniformly green on the upper surface, and air-chambers are everywhere present. In var. *aquatica* the margin of the thallus is entire or nearly so, and the upper surface completely lacks epidermal papillae or bears them very rarely; in var. *alpestris* the margin of the thallus is more or less denticulate from projecting cells, and epidermal papillae occur in greater or less abundance in the marginal portions. In var. *aquatica* the appendages of the ventral scales are entire or nearly so, and the spreading rhizoids are smooth; in var. *alpestris* the appendages are distinctly denticulate, and the spreading rhizoids tuberculate.

About fifteen years ago another so-called variety was distinguished by Hagen under the name var. *mamillata.* It was based on a supply of specimens collected by its author at Opdal in Norway and distributed by Schiffner in Hep. Europ. Exsic. *15.* Apparently Hagen himself did not publish his variety. Schiffner[11] did so, however, and quoted Hagen's original diagnosis, as follows: "Cellulae epidermicae et frondis dorsalis et carpocephali acute mamillosae." In commenting on this diagnosis Schiffner showed that the mamillose appearance, so strongly emphasized, was due to epidermal papillae and that these were restricted to the marginal portions of the thallus. He showed further that the female receptacles in all forms of *M. polymorpha* were mamillose in Hagen's sense. Var. *mamillata,* therefore, is based on exceedingly vague characters and has little or nothing to distinguish it from var. *alpestris.*

Although var. *aquatica* and var. *alpestris* are at first sight so distinct from each other they are connected by intermediate forms, and their differences seem to be associated with definite differences in environmental conditions. They represent, therefore, modifications rather than varieties in the taxonomic sense. Probably the most logical disposition to make of them is to regard them as forms, as Müller[12] has done, and to cite them as forma *aquatica* (Nees) K. Müll. and forma *alpestris* (Nees) K. Müll., respectively. Other forms, less distinct than these, might likewise be distinguished, but it would hardly be a profitable task to designate them by names.

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[11] Lotos 49: 93. 1901.

[12] Rabenhorst's Kryptogamen-Flora 6: 306. 1907.

Of the various synonyms quoted under *M. polymorpha* the first six require no special mention, since no question has arisen about them for many years. In fact three of these synonyms were never published adequately by their author at all, and nothing would now be known about them if Nees von Esenbeck had not included them among the synonyms of his varieties and forms of *M. polymorpha.* It is perhaps worthy of note, however, that *M. stellata* and *M. umbellata* were based on female and male specimens, respectively, showing how deep an impression the very different receptacles made on the early observers. The last three synonyms deserve a few words of comment.

The first, *M. vittata,* was described from specimens collected by its author on the island of Madeira. It is characterized by the presence of a longitudinal median band on the thallus, deep purple in color, and by a female receptacle bearing three to ten terete rays. The authors of the Synopsis Hepaticarum cite the species but do not number it, thus implying that they doubt its validity. They refer it with some question to one of the varieties of *M. polymorpha.* Although type specimens of *M. vittata* have not been available for study there can be little doubt that the species should be referred to *M. polymorpha* forma *aquatica,* on account of its median purple band. This conclusion is supported by the fact that Schiffner[13] quotes *M. polymorpha* var. *aquatica* definitely from Madeira, although he makes no mention of *M. vittata.* In fact the writer has found no references to the species later than the date of the Synopsis.

The next species, *M. Syckorae,* was based on female specimens collected by Syckora and by Corda in Bohemia. Nees von Esenbeck, without having seen specimens, gave a description of the species based on Corda's notes and figures. The features emphasized are the stellate female receptacles with terete rays and the monocarpous involucres, each consisting of two distinct membranes divided into six lanceolate acuminate lobes with serrate-dentate margins. In spite of the peculiarities in the involucre Nees von Esenbeck suspected that *M. Syckorae* was nothing but a form of *M. polymorpha,* and yet it is cited and numbered in the Synopsis Hepaticarum. Many years later Dědeček[14] definitely included *M. Syckorae* among the synonyms

[13] Oesterr. Bot. Zeitschr. 51: 116. 1901.

[14] Arch. Naturw. Landesdurchf. Böhmen, Bot. 5[4]: 20. 1886.

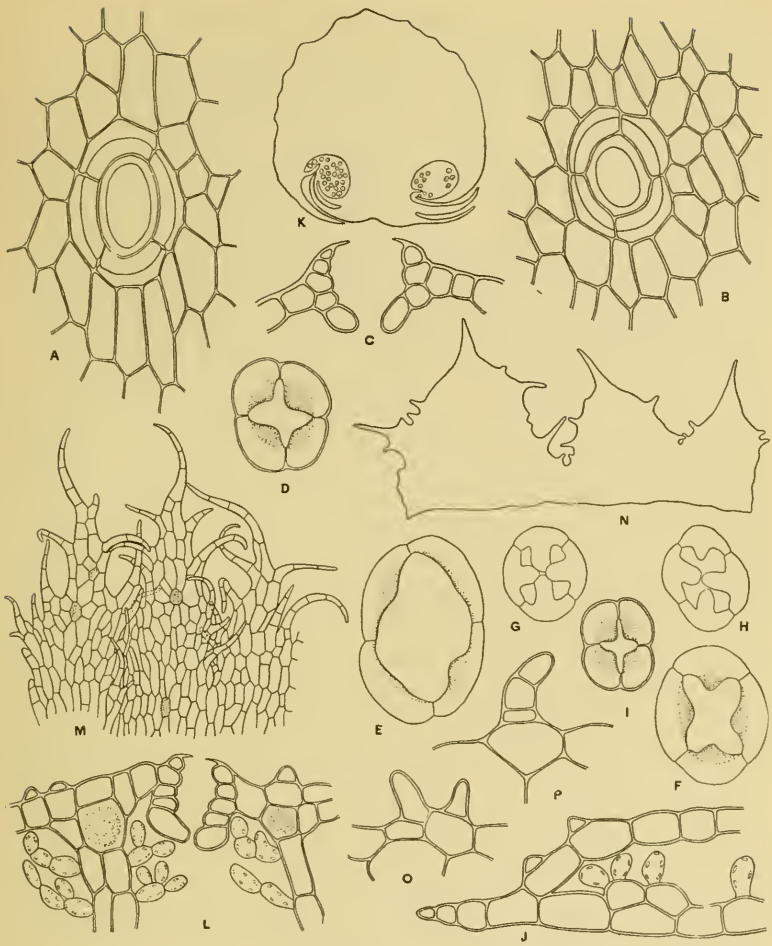

FIG. 2. MARCHANTIA POLYMORPHA L.

Anatomical details. A, B. Epidermal pores of thallus, surface view, x 225. C. Pore in cross-section, x 225. D-I. Inner openings of pores, x 225. J. Marginal portion of thallus, in section, showing two epidermal papillae, x 225. K. Stalk of male receptacle, cross-section near base, x 40. L. Female receptacle, section of part of disc, showing a pore and three epidermal papillae, x 225. M. Part of involucre, x 50. N. Part of cupule, showing three lobes, x 50. O, P. Epidermal papillae from cupule, in section, x 225. A, D. Opdal, Norway, *J. Hagen,* in V. Schiffner's Hep. Europ. Exsic. *15,* type of var. *mamillata* Hagen. B, I, J. Jamaica, *A. W. Evans.* C. Oaxaca, *E. W. Nelson 2530.* E, L-P. New Haven, Connecticut, *G. E. Nichols, A. W. Evans.* F-H. Wilbraham, Massachusetts, *E. A. Chapin,* G and H representing forma *aquatica.* K. Eberswalde, Germany, *A. W. Evans.*

of *M. polymorpha* and Schiffner[15] has since followed the same course.

The type material of the last synonym, *M. oregonensis,* consists of a series of male specimens collected on Mount Hood, Oregon, by J. Röll, in 1888. A portion of the type in the Underwood herbarium has been examined by the writer. In his original account of *M. oregonensis,* Stephani emphasizes the dentate and spinose appendages of the ventral scales and states that he knows no other *Marchantia* of temperate regions in which similar appendages occur. Howe[16] soon pointed out, however, that the appendages in many European and American specimens of *M. polymorpha* agreed with those of *M. oregonensis* and expressed the opinion that the peculiarity emphasized by Stephani had no specific significance. Fig. 1, G, drawn from *M. oregonensis,* fully supports Howe's statements. As a matter of fact the appendages are not deeply enough toothed to be called "spinose" or even "dentate"; it would be more accurate to describe them as denticulate or crenulate. In his Species Hepaticarum, published the same year as Howe's observations, Stephani[17] still maintains the validity of *M. oregonensis.* He describes the appendages as variously and remotely dentate-spinose and states that they are composed of small subequal cells. Here again Fig. 1, G brings out a slight inaccuracy, by showing that the marginal cells are distinctly smaller than the interior cells. In his critical notes he no longer emphasizes the features of the appendages but calls attention to the cruciate internal openings of the epidermal pores, stating that no other North American species has pores of this character. In the material studied by the writer no pores of a distinctly cruciate type were found; they agreed, rather, with the pores of *M. polymorpha* forma *alpestris,* as shown in Fig. 2, D. Since both of the distinctions relied upon by Stephani thus break down there seems to be no reason why *M. oregonensis* should not be considered a simple synonym of *M. polymorpha.*

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[15] Engler & Prantl, Nat. Pflanzenfam. 1^3: 37. 1893.

[16] Mem. Torrey Club 7: 62. 1899.

[17] Bull. Herb. Boissier 7: 531. 1899.

2. Marchantia plicata Nees & Mont.

Marchantia (?) *plicata* Nees & Mont.; Montagne, Ann. Sci. Nat. Bot. II. 9: 43. 1838.

Marchantia lamellosa Hampe & Gottsche; G. L. & N. Syn. Hep. 527. 1846.

Marchantia vulcanica Spruce, Trans. Bot. Soc. Edinburgh 15: 559. 1885 (as synonym).

Thallus green, not glaucous, often more or less pigmented with purple on the lower surface, usually 1-1.5 cm. wide, often 6-8 cm. long or even more, occasionally dichotomous, the successive forks usually about 2 cm. apart, texture delicate, margin entire; epidermis composed of thin-walled cells, averaging about 20μ in length and 13μ in width, papillae absent; pores (with their surrounding cells) mostly 65-80μ long and 50-60μ wide, gradually decreasing in size toward the margin, the smallest measuring about 50 x 40μ, surrounded by three or (usually) four rows of cells (two rows being in the lower series), each row being usually composed of four cells, inner opening mostly four-sided, with slightly convex to distinctly concave sides, somewhat roughened by a resinous deposit; air-chambers low, isodiametric or somewhat elongated, their boundaries very indistinct when viewed through the epidermis, everywhere present (except close to the margin), rows of photosynthetic cells usually less than three cells long; compact ventral tissue mostly twenty to twenty-five cells thick in the median portion, destitute of slime cells and sclerotic cells, the cell-walls slightly thickened and with distinct pits; ventral scales in four to six rows on each side of the thallus, median and marginal scales in distinct rows, laminar scales in two to four indistinct rows, scales often pigmented with purple, marginal scales more or less imbricated and usually projecting beyond the margin; appendages of median scales orbicular-ovate to orbicular, mostly 0.65-0.9 mm. long and 0.65-0.8 mm. wide, somewhat narrowed toward the rounded and sometimes apiculate apex, margin minutely and irregularly denticulate or crenulate, a tooth sometimes consisting of an entire cell borne on a slightly projecting stalk cell, cells rapidly decreasing in size toward the margin, median cells mostly 70-90μ in length and 40-60μ in width, marginal cells only 25-50μ in length and 12-20μ in width, cells containing oil-bodies 15-30μ in diameter, usually about ten on each appendage, restricted to submarginal portions: male receptacle borne on a stalk 2-3 cm. long, with two rhizoid-furrows, destitute of dorsal air-chambers, the disc mostly 1-1.2 cm. broad (when well developed), deeply lobed, the lobes or rays mostly eight (sometimes nine or ten), the two basal rays usually separated by a wider sinus than the others, 2-4 mm. long, rounded at the apex and with thin wavy margins, covered ventrally with

densely imbricated scales in several rows: female receptacle borne on a stalk 6-8 cm. long (when well developed), with two rhizoid-furrows and a single broad dorsal band of air-chambers, the disc mostly 1.2-1.6 cm. broad, deeply lobed, the lobes or rays spreading at maturity, mostly eleven (sometimes nine or ten), 5-6 mm. long, the two basal rays usually shorter than the others and separated by a wider sinus, rays terete, rounded at the apex, destitute of surface-papillae; involucre sometimes pigmented, deeply and irregularly lobed, the lobes long-acuminate and dentate to ciliate on the sides: spores pale yellow, 12-14μ in diameter, smooth or nearly so; elaters 3-5μ wide, bispiral: cupules deeply lobed, the lobes as in *M. polymorpha,* outer surface with epidermal papillae. (Figs. 3, 4.)

The species seems to be confined to the high mountains of South America. The following specimens have been examined:

Colombia: Boqueron, Bogota, *W. Weir* (N. Y.).

Ecuador: Quito, December, 1847, *W. Jameson* (N. Y., listed by Mitten as *M. Berteroana* in Jour. Bot. & Kew Misc. 3:361. 1851); Pichincha, *R. Spruce* (distributed in Hepaticae Spruceanae).

Peru: Cuzco, July, 1911, *H. W. Foote* (Y., listed by the writer as *M. lamellosa* in Trans. Conn. Acad. 18:299. 1914); same locality, September, 1914, *Mr. & Mrs. J. N. Rose 19060* (N. Y., Y.); Ollantaytambo, May, 1915, *Cook & Gilbert 672* (U. S., Y.); San Miguel, Urubamba Valley, June, 1915, *Cook & Gilbert 1162* (U. S., Y.); Lucumayo Valley, June, 1915, *Cook & Gilbert 1321* (U. S., Y.).

Bolivia: between Chupé and Janacaché, province of Yungas, *A. d'Orbigny 209* (M., type); Sorata, February, 1886, *H. H. Rusby 3005* in part (N. Y., listed by Spruce as *"M. plicata* Nees?" in Mem. Torrey Club 1:140. 1890); Songo, November, 1890, *M. Bang 910* (N. Y., U. S., Y., listed by Rusby as *M. polymorpha* in Mem. Torrey Club 4:274. 1895); Sorata, September, 1901, *R. S. Williams 2144* (N. Y., Y.).

The type specimen of *M. lamellosa* was collected at the following locality:

Venezuela: Paramo de Mucuchies, *Moritz 45* (listed, but erroneously ascribed to Colombia, in Syn. Hep. 527. 1846; also listed by Hampe in Linnaea 20:333. 1847).

The present species was based on a specimen without receptacles or gemmae. When originally described its generic position was considered doubtful, but the authors of the Synopsis saw clearly that it represented a *Marchantia* and suggested its

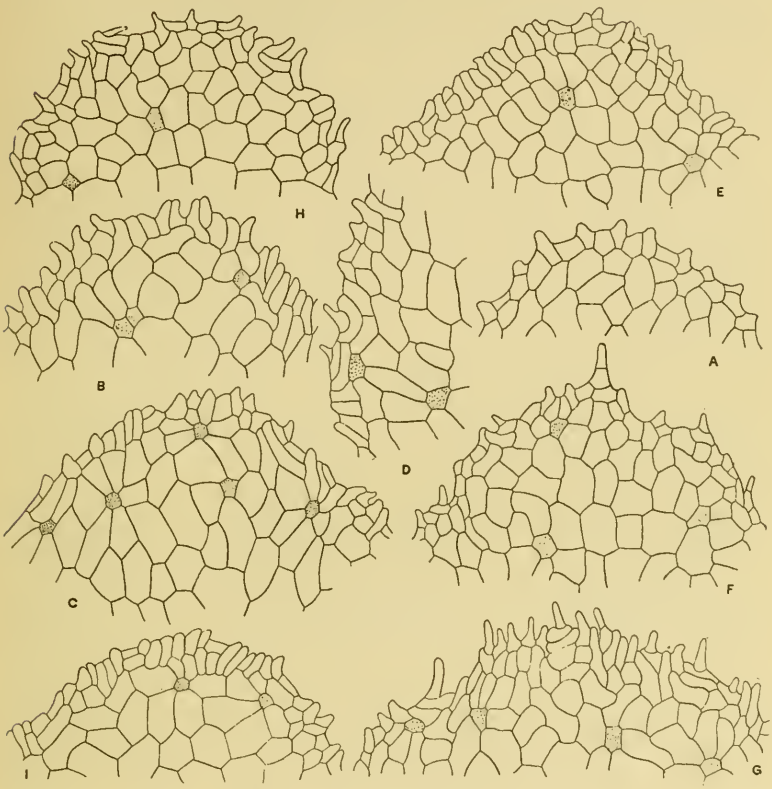

FIG. 3. MARCHANTIA PLICATA Nees & Mont.

Appendages of ventral scales, x 100. D represents the basal portion of an appendage; the other figures represent apical portions. A. Ecuador, *W. Jameson.* B-D. Peru, *H. W. Foote.* E-G. Peru, *Cook & Gilbert 672, 1162, 1321.* H. Bolivia, *A. d'Orbigny,* type. I. Bolivia, *M. Bang 910.*

relationship to *M. polymorpha.* Unfortunately the absence of receptacles made a positive conclusion impossible, and they were therefore obliged to place it among the species "incertae sedis." A portion of the type material from the Montagne herbarium, kindly forwarded by M. Paul Hariot, has been carefully com-

pared with the other specimens cited above. The epidermal cells are unusually delicate and are slightly smaller than the averages given, measuring perhaps 18 x 10μ, but the epidermal pores and ventral scales agree very closely with those of the other specimens. It is clear, therefore, in the writer's opinion, that all the specimens cited represent the same species.

The original material of *M. lamellosa* has not been available for study, but the specimen from Colombia, listed above, was referred to this species by Mitten and is evidently the same as the specimens from Ecuador, Peru, and Bolivia. On the basis of this specimen and the full description in the Synopsis Hepaticarum, *M. lamellosa* is here reduced to synonymy. It should be noted, however, that Stephani considers it valid, so that this reduction is perhaps unwarranted. He ascribes to the species cruciate pores and papillate rays on the female receptacles. In one of the Peruvian specimens, No. 672, some of the pores are as cruciate as those of *M. oregonensis,* but other pores are not cruciate at all, so that a considerable range of variation is present. The lack of receptacles in these specimens makes it impossible to determine whether papillate rays are associated with pores which approach the cruciate condition, although the constant absence of papillae in all the fruiting specimens studied, which are clearly the same as No. 672, makes such an association improbable. Even if papillae occasionally occurred they would hardly afford a basis for a specific separation. Stephani cites *M. lamellosa* from the type locality and also from Ecuador (Chimborazo and Altar, *Hans Meyer*).[18] He cites *M. plicata* from the type locality, from Ecuador (Quito, *Ortoneda, Spruce*), from Colombia (*Lindig*), and from Venezuela (Merida, *Moritz*). It is probable that the Lindig specimens are those listed by Gottsche under *M. polymorpha* and that the Moritz specimens are those doubtfully referred by Hampe[19] to *M. Berteroana.* Of course, in the absence of the specimens themselves, this matter can not be definitely decided.

Although *M. plicata* and *M. polymorpha* are closely related species it is usually easy to distinguish them. Some of the differential characters, however, are vague and subject to variation. When *M. plicata* is well developed the thallus and the

[18] See Meyer, In den Hoch-Anden von Ecuador 517. Berlin, 1907.
[19] Linnaea 20: 333. 1847.

sexual receptacles are larger than in the most robust forms of *M. polymorpha,* approaching or equalling in this respect the more southern *M. Berteroana.* The thallus also shows a tendency to fork at infrequent intervals, so that it presents the appearance of being more elongated than in *M. polymorpha.*

The lack of epidermal papillae on the rays of the female receptacle seems also to be a distinguishing character. In fact

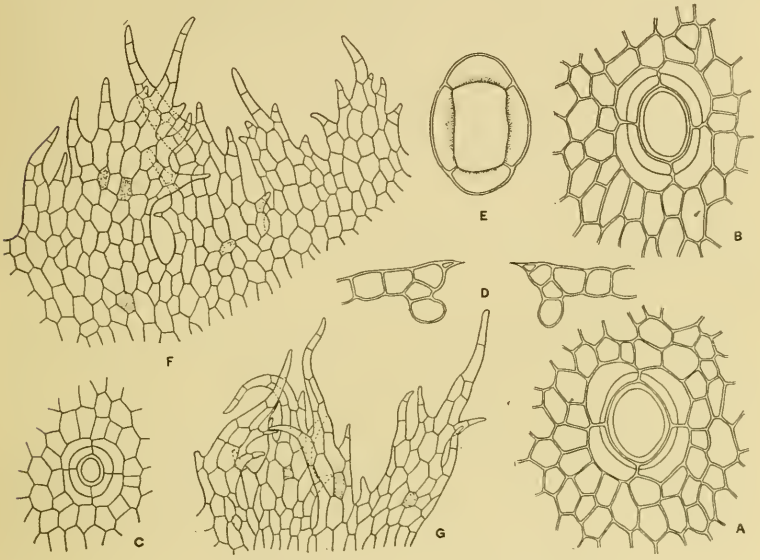

FIG. 4. MARCHANTIA PLICATA Nees & Mont.

Anatomical details. A-C. Epidermal pores of thallus, surface view, x 225. D. Pore in cross-section, x 225. E. Inner opening of pore, x 225. F, G. Two parts of the same involucre. A, B, D, E. Peru, *Cook & Gilbert 1162, 1321.* C. Bolivia, *A. d'Orbigny,* type. F, G. Colombia, *W. Weir.*

papillae of this type are restricted to the outer surface of the cupules. In spite of the large size of the thallus the epidermis of *M. plicata* is unusually delicate in texture and the air-chambers unusually low.

The ventral scales exhibit considerable variation with respect to size and amount of pigmentation. In typical examples the ventral surface is almost covered with purple scales, but this condition is by no means constant; the scales may only partially cover over the surface and the pigmentation may be very slight.

The crowded marginal scales, however, visible from above, seem to be a constant feature, although these scales may not be any more conspicuous than in *M. polymorpha.* The appendages of the ventral scales, as in other species, yield some of the most important characters (Fig. 3). The small marginal cells are exceedingly irregular, forming various angles with the periphery of the appendage and often projecting in the form of blunt teeth. Frequently a projecting cell will be borne on a broader basal cell, a two-celled tooth of a peculiar type being thus produced. Usually the difference in size between the marginal cells and the interior cells is very marked, but the difference is less when the appendages are poorly developed (Fig. 3, A). The apices of the appendages are especially variable. In some cases a distinct apical tooth two cells long is present, making the appendage apiculate (Fig. 3, F); in other cases the apical tooth is hardly distinguishable from the neighboring teeth (Fig. 3, G); in still other cases there is no indication whatever of an apical tooth (Fig. 3, H, I).

When the appendages are compared with those of *M. polymorpha* they are found to have many features in common. In both species they are similar in form and show a decrease in the size of the cells in passing from the middle to the margin; in both species the apex is variable and the margin is normally denticulate. In *M. plicata,* however, the cells are larger and the decrease in size more abrupt, the denticulation tends to be more pronounced, owing largely to the frequency of two-celled teeth, and the marginal cells tend to be more irregular. Although these differences are of a comparative nature and subject to variation, they will usually be found serviceable in separating the species.

3. Marchantia Berteroana Lehm. & Lindenb.

Marchantia Berteroana Lehm. & Lindenb.; Lehmann, Pug. Plant. 6: 21. 1834.

Marchantia tabularis Nees, Naturg. Europ. Leberm. 4: 71 (footnote). 1838.

Marchantia cephaloscypha Steph. Hedwigia 22: 51. 1883.

Thallus green or bluish green, sometimes glaucous, often more or less pigmented with purple or brownish near the margin and on the lower surface, usually 1-1.5 cm. wide and 6-8 cm. long,

variously dichotomous, the successive forks sometimes 2-3 cm. apart but often closer together, texture usually tough and leathery, margin entire or minutely and irregularly denticulate or crenulate, more or less plicate; epidermis composed of cells with thin or slightly thickened walls, mostly 20-60μ long (averaging about 32μ) and 16-24μ wide (averaging about 19μ), papillae absent; pores (with their surrounding cells) mostly 60-80μ long and 50-60μ wide, surrounded usually by six rows of cells (three in each series), each row being usually composed of four cells, inner opening cruciate, the bounding cells commonly four (rarely three or five), slightly roughened; air-chambers of medium height, usually a little longer than broad, their boundaries indistinct when viewed through the epidermis, present everywhere, rows of photosynthetic cells usually three or four cells long; compact ventral tissue about twenty-five cells thick in the median portion, destitute of slime cells and sclerotic cells, usually thin-walled and with indistinct pits; ventral scales in two rows, median and laminar, no marginal scales being present, scarcely imbricated, pale or brownish; appendages of median scales orbicular-ovate to broadly orbicular, usually somewhat narrowed toward the rounded apex, mostly 0.6-1 mm. in length and about the same in width, margin minutely and often regularly crenulate or denticulate from projecting cells, cells showing an abrupt decrease in size toward the margin, median cells mostly 60-85μ long and 20-40μ wide, marginal cells (in one, two, or three rows) mostly 12-20μ long and 8-12μ wide, cells containing oil-bodies about 20μ in diameter, about five on each appendage, restricted to submarginal portions: male receptacle borne on a stalk 1-5 cm. long with two rhizoid-furrows, destitute of dorsal air-chambers, the disc about 1 cm. in diameter, more or less deeply lobed when well developed, the lobes or rays mostly eight, usually 2-3 mm. long, rounded at the apex and with thin wavy margins, covered ventrally (except in the marginal portions) with imbricated scales in several rows, sinuses usually subequal in width: female receptacle borne on a stalk mostly 3-8 cm. in length, with two rhizoid-furrows and a broad dorsal band of air-chambers, the disc mostly 0.8-1 cm. broad, deeply lobed, the lobes or rays spreading at maturity, mostly nine, 2-3 mm. long, separated by subequal sinuses, terete, rounded, destitute of epidermal papillae; involucre much as in *M. polymorpha:* spores brownish yellow, mostly 8-10μ in diameter, smooth; elaters about 5μ wide, bispiral: cupules deeply lobed, the lobes as in *M. polymorpha,* outer surface with epidermal papillae. (Fig. 5.)

A widely distributed species, restricted (according to our present knowledge) to the Southern Hemisphere. The following South American specimens have been examined:

Argentina: Buenos Aires, without date, *Twiedie* (H.); La Plata, collector and date unknown (H.).

Chile: Concepcion, November, 1905, *R. Thaxter, 16, 66* (H., Y.); Port Corral, January, 1906, *R. Thaxter, 62, 74, 92* (H., Y.); Hermite Island, Cape Horn, 1843, *J. H. Hooker* (H.).

Juan Fernandez: without definite localities, 1830, *C. Bertero* (H., N. Y.), type); *H. N. Moseley* (N. Y., Challenger Expedition); 1901, *G. T. Hastings 218* (N. Y., U. S.).

Falkland Islands: without definite locality, 1843, *J. D. Hooker* (H.).

The following specimens from other regions have likewise been examined:

St. Helena: without definite locality or date, *J. Melliss* (N. Y.); 1844, *J. D. Hooker* (N. Y.); February, 1890, *W. H. & A. H. Brown 264* (U. S., United States Eclipse Expedition to Western Africa, listed as *M. tabularis* by Stephani in Bull. Herb. Boissier 7: 1899).

Cape Colony: Table Mountain, *F. Krauss* (N. Y.); Montague Pass, *J. C. Bruetel* (N. Y.); without definite localities or dates, *W. H. Harvey* (N. Y.), *Capt. Rabenhorst* (Y.).

Australia: Victoria, *Robertson 633* (N. Y.); Swan River, 1846, *J. Drummond* (H.); without definite locality, *F. von Müller* (H., Y.).

Tasmania: without definite localities, 1823, *Lawrence* (N. Y.); 1838, *R. Gunn* (N. Y.); no date, *W. Archer* (N. Y.); western mountains, no date, *Lawrence* (N. Y.); Tasman Peninsula, roadside from Long Bay to Tarrand, February, 1899, *1956b* (H., distributed by E. Levier as *M. cephaloscypha*).

New Zealand: without definite localities, no date, *A. Sinclair* (N. Y.); 1881, *E. Craig* (Y.); no date, *J. Remy* (N. Y., distributed by C. Roumeguere as *M. nitida*); Waikehi, *A. Sinclair* (H.); Raipara, 1850, *S. Mossmann* (H.); Point Cooper, collector and date unknown (N. Y.); North Island, 1904, *W. A. Setchell 32* (Y.); Lord Auckland's Group, November, 1840, *J. D. Hooker* (H.); Campbell Island, November, 1840, *J. D. Hooker* (H.); without definite locality, date, or collector's name (B., type of *M. cephaloscypha*).

Other South American stations of interest, cited in the literature, are the following:

ARGENTINA: Staten Island, Tierra del Fuego, *C. Spegazzini* (listed by Massalongo in Nuovo Gior. Bot. Ital. 17: 258. 1885).

CHILE: San Augustin and San Francisco del Monte, *F. J. F. Meyen* (listed in Syn. Hep.); Otway Gulf, *P. Savatier* (listed and figured as *M. tabularis* by Bescherelle and Massalongo in Compt. Rend. Miss. Sci. Cap Horn 5: 247. *pl. 4, f. 17.* 1889).

The identity of *M. Berteroana* and *M. tabularis* was established by Schiffner, although Nees von Esenbeck, in proposing *M. tabularis,* recognized its close relationship with the older species. *M. Berteroana* was based on specimens collected by Bertero on the island of Juan Fernandez, while the type material of *M. tabularis* came from Table Mountain in Cape Colony. The Synopsis Hepaticarum recognizes both species; it cites *M. Berteroana* from Chile and St. Helena, as well as from the type locality, and gives Devil's Peak in Cape Colony as a second station for *M. tabularis.* Under *M. Berteroana* three varieties are recognized: α, from Juan Fernandez, β, *biflora,* from Chile; and γ, *anactis,* from Juan Fernandez and St. Helena. In α, according to the description, the rays of the female receptacle are one third longer than the involucres, the latter enclosing three to five flowers; in β, the rays are the same as in α but are fibrillose, while the involucres usually contain only two flowers; in γ, the rays do not project beyond the involucre at all.

In discussing *M. Berteroana,* Schiffner[20] points out that the differences relied upon by Nees von Esenbeck in separating *M. tabularis* are of no significance and that the same thing is true of the differential characters assigned to the three varieties of *M. Berteroana.* He points out further certain mistakes in the original description of this species and also in the description given in the Synopsis. He based his conclusions on a large series of original and authentic specimens, several of which have been studied by the present writer, and there seems to be no reason for doubting the accuracy of his observations.

Schiffner was apparently the first to give a satisfactory description of the scale appendages in *M. Berteroana.* He calls attention to the finely crenulate margin, to the border of very small cells in one or two rows, and to the sharp distinction in size between

[20] Oesterr. Bot. Zeitschr. 46: 41-44, 100-103. 1896.

the marginal cells and the cells which adjoin them. To *M. polymorpha* he assigns appendages which are minutely but sharply denticulate, and adds that the cells gradually increase in

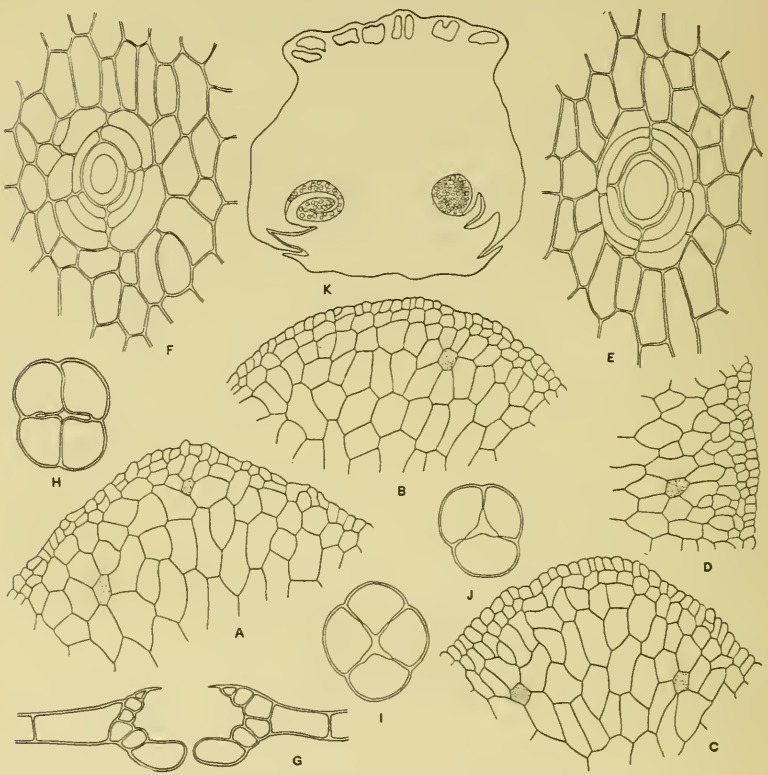

Fig. 5. Marchantia Berteroana Lehm. & Lindenb.

Appendages of ventral scales and other anatomical details. A-D. Appendages of ventral scales, x 100: D represents the basal portion of an appendage; the other figures represent apical portions. E, F. Epidermal pores of thallus, surface view, x 225. G. Pore in cross-section, x 225. H-J. Inner openings of pores, x 225. K. Stalk of female receptacle, cross-section near base, x 40. A. Juan Fernandez, *G. T. Hastings 218.* B, E, G, H. Chile, *R. Thaxter 66.* C, D. Cape Colony, *Capt. Rabenhorst.* F, I-K. Australia, *F. von Müller.*

size in passing from the margin to the median portion. In most cases the distinctions given by Schiffner apply very definitely, but in the forma *aquatica* of *M. polymorpha* (Fig. 1, E, F) the appendages are usually destitute of distinct denticulations, the

entire or crenulate margin closely simulating that of *M. Berteroana*. Even here, however, the gradual decrease in the size of the cells as the margin is approached is in contrast to the abrupt decrease found in *M. Berteroana*.

In habit and in general appearance *M. Berteroana* resembles *M. polymorpha* very closely, and it is not surprising that the early observers failed to distinguish it as a species. The thallus, to be sure, is more robust, it tends to be thicker and more leathery than in the northern species, and the rays of the female receptacle tend to be shorter, but these differences are not always pronounced. There are, however, several distinctive features, in addition to the scale-appendages, which deserve to be emphasized. In the first place *M. Berteroana* seems to lack marginal scales altogether. Sometimes the laminar scales form a vague double row, some of the scales being nearer the margin than the others, but even under these conditions there is quite a little space between the outermost scales and the margin. In most cases the row of laminar scales is more definite and the region without scales is consequently wider. In *M. polymorpha* the marginal scales are apparently always present, although they do not always attain the same degree of development. *M. Berteroana* is further distinguished by its cruciate epidermal pores, and by its lack of epidermal papillae on both thallus and female receptacle. The lack of marginal scales, the crenulate scale appendages, and the cruciate pores will serve also to distinguish *M. Berteroana* from *M. plicata,* although there is no evidence as yet that their ranges overlap.

The writer has fortunately been able to examine an original specimen of *M. cephaloscypha*. The species was based on gemmiparous material with young female receptacles collected somewhere in New Zealand, neither the date nor the collector's name being given. A few years later Stephani[21] referred to his species a series of specimens from various parts of Australia and was able to add the characters derived from mature female receptacles and ripe capsules. In his Species Hepaticarum,[22] in addition to New Zealand and Australia, he cites Tasmania, Fuegia, Patagonia and Chile as localities for the plant and notes that it is not

[21] Hedwigia **28**: 265. 1889.
[22] Bull. Herb. Boissier **7**: 391. 1899.

rare. Still later he[23] quotes stations on Juan Fernandez, the Chilean island of Chiloé, and the Falkland Islands. He therefore gives the species a very extensive distribution in the Southern Hemisphere. It has already been noted that he does not credit *M. Berteroana* to America at all, the only specimens which he cites being from Cape Colony, the Transvaal, and the island of St. Helena.

In his descriptions of *M. cephaloscypha* Stephani emphasizes the cruciate pores, the large scale-appendages bordered with very small cells, the nine-rayed female receptacles with smooth and terete rays, the eight-lobed male receptacles, and the spinose cupules. It will at once be noted that all of these features are found in *M. Berteroana.* There are, however, certain discrepancies between Stephani's descriptions and the account of *M. Berteroana* given above. He states, for example, in his original description that the cupules are contracted at base and apex and that the ventral scales are in three rows on each side of the thallus, one row of tongue-shaped scales being close to the margin. In his last description he still emphasizes the contracted apices of the cupules but makes no allusion to the three rows of ventral scales, perhaps because he has already given a triseriate arrangement of the scales as a generic character.

The type specimen shows that some of the specific characters emphasized by Stephani are based on misconceptions. The single cupule present, for example, is contracted at the throat but flares widely at the mouth. Even if the mouth itself were contracted this condition might easily be due to immaturity and figures of a young cupule of *M. polymorpha* by Mirbel,[24] in which the mouth is distinctly contracted, fully support this view. There are, moreover, no marginal ventral scales, although the margin, being irregularly crispate, produces the effect of scales. The appendages of the median scales are slightly crenulate and show one or two rows of marginal cells, the rays number nine in the female receptacle and are destitute of papillae, the surface of the cupule bears numerous papillae, and the pores are of the cruciate type. The writer therefore feels justified in considering *M. cephaloscypha* a simple synonym of *M. Berteroana.*

[23] Kungl. Svensk. Vetensk.-Akad. Handl. 46[9]: 5. 1911.
[24] Mém. Acad. Sci. 13: *pl. 4, f. 31, 32.* 1835.

Section II. Chlamidium

4. Marchantia paleacea Bertol.

Marchantia paleacea Bertol. Opus. Sci. Bologna 1: 242. 1817.
Marchantia papillata β italica Raddi, Mem. Soc. Ital. Modena 19: 44. 1823.
Fimbriaria paleacea Corda; Opiz, Beitr. zur Naturg. 648. 1828.
Fegatella Michelii Corda, *l. c.* 649. 1828 (according to Nees von Esenbeck).
Marchantia nepalensis Lehm. & Lindenb.; Lehmann, Pug. Plant 4: 10. 1832.
Marchantia nitida Lehm. & Lindenb. *l. c.* 11. 1832.
Marchantia squamosa Raddi; Lehm. & Lindenb. *l. c.* 12. 1832 (as to the East Indian plant).
Marchantia tholophora Bisch. Nova Acta Acad. Leop.-Carol. 17: 989. 1835.
Marchantia calcarata Steph. Bull. Herb. Boissier 5: 98. 1897.
Marchantia planipora Steph. *l. c.* 98. 1897.

Thallus pale green, often glaucous, sometimes more or less pigmented with purple, especially near the margin and on the lower surface, usually 0.5-0.8 cm. wide and 2-4 cm. long, repeatedly dichotomous, the successive forks usually 1 cm. or less apart; texture firm but scarcely leathery, margin entire; epidermis composed of cells with more or less thickened walls, sometimes in two layers, mostly 35-70μ long (averaging about 43μ) and 20-40μ wide (averaging about 30μ), papillae absent; pores (with their surrounding cells) mostly 70-90μ long and 65-85μ wide, sometimes measuring as much as 140 x 100μ, surrounded usually by six (or seven) rows of cells (three in the upper and three or four in the lower series), each row being usually composed of four cells or the innermost row of the upper series of from four to eight cells, inner opening cruciate, the bounding cells smooth; air-chambers usually high, isodiametric or slightly elongated, their boundaries indistinct when viewed through the epidermis, present everywhere, rows of photosynthetic cells often six or seven cells long but sometimes shorter; compact ventral tissue mostly twenty to thirty cells thick in the median portion, the walls sometimes pigmented, more or less thickened and showing distinct pits, sclerotic cells usually distinct, scattered, ten to twenty in a cross-section of thallus, more abundant in median region but not confined to this, slime-cells sometimes lacking, sometimes more or less abundant, especially toward the margin; ventral scales in two distinct rows, the laminar scales alternating with the median and only a little nearer

the margin; appendages of median scales oblong, ovate, or ovate-orbicular, mostly 0.6-0.75 mm. long and 0.45-0.6 mm. wide, usually narrowed toward the rounded, obtuse or acute apex, margin entire or vaguely and irregularly denticulate or dentate, rarely with a basal lobe, cells showing a slight and gradual decrease in size toward the margin, median cells isodiametric to distinctly longer than broad, mostly 25-60μ long and 20-30μ wide, marginal cells mostly 30-40μ long and 12-20μ wide, very irregular, the long axis sometimes parallel with the margin and sometimes at an angle with it, cells containing oil-bodies sometimes absent altogether, when present about 20μ in diameter, one to three or more in number and indefinite in position: male receptacle borne on a stalk 5-7 mm. high, with two rhizoid-furrows, destitute of dorsal air-chambers, the disc 5-6 mm. broad, very shortly or sometimes (according to Schiffner) more deeply eight- (to twelve-) lobed, the lobes or rays rounded and with a thin wavy margin, ventral scales restricted to middle portion of disc: female receptacle borne on a stalk 2-4 cm. high, with two rhizoid-furrows and a single broad dorsal band of air-chambers, the disc about 0.5 cm. broad, usually nine-lobed, the lobes or rays spreading at maturity, 0.8-1.2 mm. long, separated by subequal sinuses or with the deep sinus between the basal ray broader than the others, flat, dilated at the truncate or emarginate apex, disc with a median hemispherical or papilliform protuberance about 0.5 mm. in diameter and nine distinct ridges corresponding with the rays; involucre much as in *M. polymorpha:* spores brownish yellow, about 34μ in diameter, with a narrow hyaline margin about 2μ wide, outer face bearing a series of low lamellae sometimes forming an indistinct reticulum; elaters mostly 6-8μ wide, bispiral; cupules with toothed lobes much as in *M. polymorpha,* but lacking epidermal papillae. (Figs. 6-8.)

A widely distributed species in tropical and subtropical regions. The following North American specimens have been examined:

Arizona: Huachuca Mountains, 1910, *L. N. Gooding 824* (N. Y.).

Puebla: Puebla, 1906, *Frère Arsène* (N. Y.); Honey Station, October, 1908, *Barnes & Land 507* (Y.); banks along Avenida Hidalgo and path to barranca, Tezuitlan, *Barnes & Land 544* (Y.); Santa Barbara, near Puebla, November, 1909, *Frère Nicolas 3* (Y.).

Vera Cruz: Orizaba, 1855, *F. Müller 2245* in part (N. Y.); walls of Lost River sink, Orizaba, November, 1908, *Barnes & Land 668* (Y.).

Guatemala: Coban, Alta Verapaz, 1310 m. alt., 1892, *H. von Tuerckheim 4960* (N. Y.).

Cuba: without definite locality, *C. Wright* (H., N. Y., Y., distributed in Hep. Cubenses as *M. domingensis*); La Perla, Oriente, 600-660 m. alt., February, 1911, *J. A. Shafer 9096* (N. Y., Y.); Monte Verde, Oriente, on walls of the ruined mansion of Lescaille, where Wright lived, August, 1913, *Brother Leon 4089* (N. Y.).

Jamaica: Whitfield Hall Plantation, December, 1896, *W. Harris 11063* in part (N. Y.); along path from Cinchona to Clyde River, July, 1903, *A. W. Evans 14* (Y.); vicinity of Cinchona, February, 1905, *C. E. Cummings 29, 31* (N. Y., Y.); Mabess Road, May, 1906, *D. S. Johnson 46* (Y.); Morce's Gap and vicinity, August, 1906, *A. W. Evans 462* (Y.).

The following specimens from Europe, the Azores, and Asia have likewise been examined:

France: Mentone, November, 1864, *I. T. Moggridge* (N. Y.).

Italy: without definite locality, *G. Raddi* (N. Y., labeled *M. papillata β italica*); Monte Oliveto, near Pegli in Liguria, May, 1851, *L. Caldesi* (N. Y.); near Genoa, May, 1855, *G. de Notaris* (N. Y., also distributed in Rabenhorst's Hep. Europ. *27*); Ripoli, near Florence, May, 1899, *E. Levier* (Y., Micheli's locality); Trezzo sull' Adda, province of Milan, July, 1899, *F. A. Artaria* (C. C. H.; also distributed in Schiffner's Hep. Europ. Exsic. *13*).

Azores: San Miguel 1865, *F. D. Godman* (N. Y.); August, 1894, *C. S. Brown, 365* (N. Y.), *366* (N. Y.); August, 1894, *W. Trelease 1320* (N. Y.), *1321* (N. Y.); May and June, 1898, *B. Carriero 713, 718* (Y.). The specimens collected by Brown and Trelease have been listed by Trelease in Rept. Missouri Bot. Gard. **8**: 187. 1897. The following specimens, however, although listed under *M. paleacea,* should be referred to *Conocephalum conicum* (L.) Dumort.: *C. S. Brown 367* (from San Miguel), *368* (from Fayal), *369* (from Pico) and *W. Trelease 1317* (from Terceira). A specimen collected by B. Carriero at Furnas, in 1888, has been reported by Schiffner in Oesterr. Bot. Zeitschr. **51**: 116. 1901.

China: Szechwan, no date, *E. Faber 1110* (N. Y.).

India (including Nepal): Northwest Himalayas, no date, *H. Falconer 1073* (N. Y., U. S., Y.); *J. F. Royle* (N. Y.); Nepal, *N. Wallich* (N. Y., types of *M. nepalensis, M. nitida,* and *M. squamosa*); Shagak Valley, 1847, *T. Thomson 1661, 1663* (N.

Y.); Kumaon, *Strachey & Winterbottom* (N. Y., listed by Strachey, as *M. paleacea* and *M. nitida,* in Cat. Pl. Kumaon, 234. 1906); Musooric (Northwest Himalayas), Arnigadh, December, 1895, *W. Gollan 210* (N. Y., Y., distributed by E. Levier as *M. nepalensis*).

Japan: Nagasaki, April-May, 1875, *R. Oldham* (N. Y., listed by Mitten, as *M. nitida,* in Trans. Linn. Soc. II. Bot. 3:205. 1891); Kigo, August, 1877, *Ahlberg* (B. type of *M. planipora*); Yamakita, Spidzuoka, May, 1899, *Abbé Faurie* (Y., distributed as *M. nitida* in Hép. du Japon *82*); Tokyo, May, 1897, *K. Miyake 40* (C. C. H., Y., determined as *M. diptera*); Kuzunmura, August, 1898, *K. Okudaira 26* (C. C. H); Kyoto, August, 1900, *K. Miyake* (Y., determined as *M. planipora*); Mt. Futatabisan, near Kobe, April, 1903, *Abbé Faurie* (Y., distributed as *M. diptera* in Hép du Japon *1268*); Jigokudani, May, 1903, *S. Okamura* (C. C. H.); Kochi, May, 1904, *S. Okamura* (C. C. H.); Kanagawa, Sagami, no date, *M. Maeda 41* (Y.); Osaka, May, 1905, *S. Okamura* (C. C. H.); Ikku, May, 1908, *S. Okamura* (C. C. H.).

Java: Mt. Pangerango, April, 1894, *V. Schiffner* (Y., distributed as *M. nitida* in Iter Ind. *59*).

Within recent years *M. paleacea* has been recorded from the Caucasus, from Dalmatia, Spain and Portugal, and from Morocco. Although the writer has seen no specimens from any of these countries, there can be little doubt regarding the correctness of the determinations. Some of the records for *M. nitida,* however, are open to suspicion. This species has been reported from the Philippines, Tahiti, Samoa and New Zealand, as well as from the Fiji and Hawaiian Islands. Specimens from the first four of these localities, which have been determined as *M. nitida,* have been examined and are, in the writer's opinion, referable to other species. No specimens from either the Fiji or the Hawaiian Islands have been available for study.

Although *M. paleacea* is here reported from a number of North American localities it is remarkable that there are no earlier records for the species from America. In fact the only trustworthy records for *M. tholophora,* here considered a synonym of *M. paleacea,* are the following:

Oaxaca: near Oaxaca, *Sommerschu* (the type-locality); Chinantla, *F. Liebmann* (listed by Gottsche in Mex. Leverm. 1863).

It has already been noted that *M. paleacea* was distinguished by the Florentine botanist Micheli as long ago as 1729. His

Fig. 6. Marchantia paleacea Bertol.

Ventral scales, x 27. A-G represent median scales (with appendages); H-O, laminar scales (without appendages). A-D, H-J. Italy, *F. A. Arteria,* in V. Schiffner's Hep. Europ. Exsic. 13. E, K. Vera Cruz, *Barnes & Land 668.* F, L. Cuba, *C. Wright,* in Hep. Cubenses, as *M. domingensis.* G, M-O. Java, *V. Schiffner,* in Iter Ind. 59, as *M. nitida.*

figure brings out clearly the general habit of the plant and many of the features of the cupules and female receptacles. The rays of the latter are shown to be flat at their extremities, and the center of the disc is marked by a distinct rounded elevation. In the only receptacles where the rays can be counted ten or eleven are represented, but one receptacle in profile shows only four rays, indicating that sometimes at least fewer than ten rays were present in the material figured. It is now admitted that the

normal number of rays is nine. Micheli, in his description, emphasizes the glaucous color of the thallus. The species is still abundant in the vicinity of Florence, where it was originally collected, and specimens from this region are among those cited above.

Bertolini's description is drawn from female plants, and he distinctly states that both male receptacles and cupules were unknown to him. His material came from the vicinity of Chiavari in Liguria. He adds very little to Micheli's account, but gives the number of rays definitely as ten and notes that their extremities are obtuse or almost truncate. Apparently his species was not very widely known at first because neither Raddi nor Lehmann and Lindenberg make any allusion to it. Raddi's *M. papillata β italica* was based on Micheli's description and figure and on specimens collected at Micheli's original locality. *M. nepalensis* and *M. nitida* were based on material collected by Wallich in Nepal and *M. squamosa* on two specimens, one collected by Wallich in Nepal and the other by Raddi in Brazil.

In 1835 Taylor[25] accepted *M. paleacea* as a species and referred to it not only the Italian specimens originally cited but also specimens from Nepal collected by Wallich. Although there seem to be no specimens in the Taylor herbarium labeled *"M. paleacea"*, there are two with a manuscript name of Taylor's from the Wallich collection. In one case *M. nitida* is given as a synonym and *M. squamosa* as a doubtful synonym, so that these specimens probably represent the *M. paleacea* of Taylor's paper. Unfortunately his figures and description do not correspond in all respects with authentic specimens of the species in question and have therefore given rise to considerable confusion. The most marked discrepancy is in his account of the female receptacles, where the number of involucres is given as four to six, instead of eight (corresponding with nine rays), but an error of this sort might easily be made if poor material was examined. Taylor's specimens are, indeed, imperfectly developed, but they show the thallus characters of *M. paleacea* very clearly, and his determination may therefore be considered correct.

In proposing *M. tholophora* as a species Bischoff makes no mention of *M. paleacea* or of the various species based on

[25] Trans. Linn. Soc. 17: 378. *pl. 12, f. 3.* 1835.

Wallich's specimens, so that the works of Bertolini and of Lehmann and Lindenberg may have been unknown to him. His description was drawn from Sommerschu's material, collected

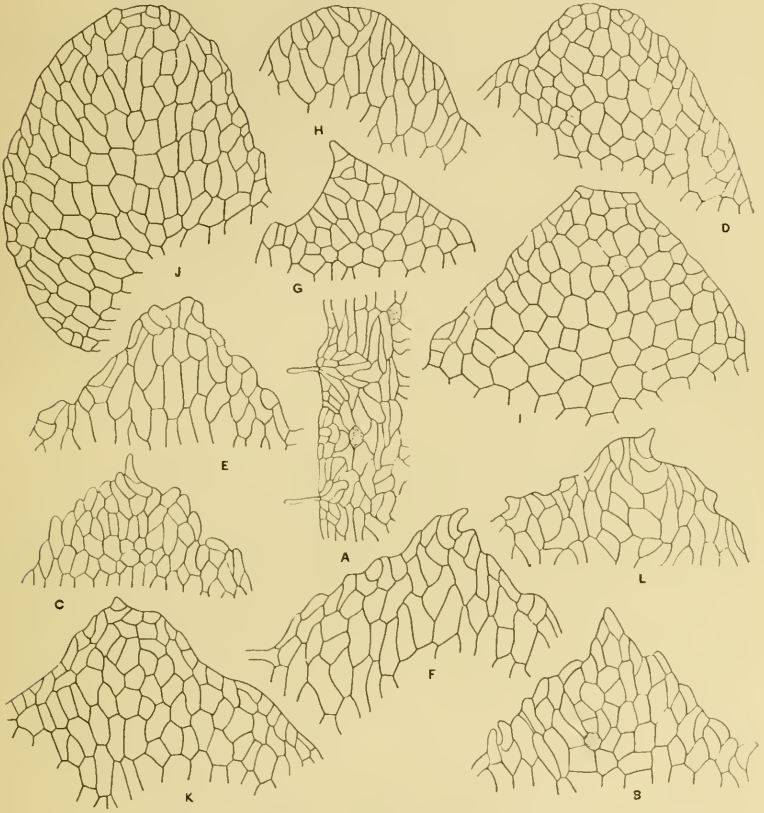

FIG. 7. MARCHANTIA PALEACEA Bertol.

Portions of ventral scales. A. Margin of basal portion of median scale, x 100. B-L. Appendages of median scales, x 100. A-C. Italy, *F. A. Artaria,* in V. Schiffner's Hep. Europ. Exsic. *13.* D. Azores, *F. D. Godman.* E, F. Vera Cruz, *Barnes & Land 668.* G, H. Cuba, *C. Wright,* in Hep. Cubenses, as *M. domingensis.* I-K. Nepal, *N. Wallich;* I, type of *M. nepalensis;* J, type of *M. nitida;* K, type of *M. squamosa;* L, Java, *V. Schiffner,* in Iter Ind. *59,* as *M. nitida.*

near Oaxaca, Mexico, and is unusually detailed. The species is recognized as valid by subsequent writers, the authors of the Synopsis Hepaticarum placing it next to *M. nitida* and Stephani following their example. The original material has not been available for study. Bischoff's description, however, and the

figure which he[25] afterwards published show almost beyond a doubt that the species represents a synonym of *M. paleacea.* This conclusion seems further warranted by the fact that the true *M. paleacea* is now known from several Mexican localities.

Nees von Esenbeck, in describing *M. paleacea,* places it in the section *Chlamidium* and calls especial attention to the features of the female receptacle. He gives the normal number of rays as nine and mentions the median protuberance of the disc and the dilated apices of the rays. Among the synonyms of the species he includes *M. nitida* without question, basing his opinion on specimens received directly from Lindenberg. He quotes a statement of the latter author to the effect that *M. nitida* is very close to the Italian *M. paleacea* and perhaps identical with it, accompanied by the remark that *M. paleacea* had not been seen by him when he published *M. nitida* as a new species. Nees von Esenbeck hesitates somewhat in the case of Taylor's *M. paleacea* but inclines toward the opinion that this plant also must be the same as Bertolini's species.

In spite of these statements *M. nitida* is reinstated as a valid species in the Synopsis Hepaticarum and Taylor's *M. paleacea,* so far as the Nepal specimens are concerned, is given as a synonym under it, the range of *M. paleacea* being again restricted to Italy. Both *M. nepalensis* and *M. squamosa* are likewise accepted as valid and these two species, together with *M. paleacea* and *M. nitida,* are included under the section *Chlamidium.* Many years later, in 1899, Stephani,[27] in recognizing these four species, placed *M. nitida* and *M. nepalensis* in his section with unsymmetrical receptacles, while he placed *M. paleacea* and *M. squamosa* in the section with symmetrical receptacles.

In 1898 doubt was again thrown on the validity of *M. nitida* by Schiffner,[28] who stated that it was probably synonymous with *M. paleacea.* Two years later he reaffirmed this idea and added that *M. calcarata* Steph., according to a specimen in his herbarium, was surely identical with *M. nitida.*[29] In the following year

[26] Handb. Bot. Term. und Systemk. 2: *pl. 55, f. 2727.* 1842.

[27] Bull. Herb. Bossier 7: 402, 522. 1899.

[28] Conspect. Hepat. Archip. Indici 50. Batavia, 1898.

[29] Fl. de Buitenzorg 4: 31. 1900. A specimen in the writer's herbarium, collected by the Abbé Faurie at Tokyo, Japan, and distributed (Hép. du Japon *2360*) under the name *M. calcarata,* represents *M. polymorpha.* Stephani himself now regards the true *M. calcarata* as a synonym of *M. diptera* Mont., a species which evidently requires further study.

he maintained still more definitely that *M. paleacea* and *M. nitida* were identical and stated further that in his opinion *M. nepalensis* also would have to be considered a synonym.[30] He criticised Stephani for placing *M. paleacea* in one section of the genus, while he placed *M. nepalensis* and *M. nitida* in another, thus implying that their relationship to the Italian species was at best remote.

The writer would agree with Schiffner in his reductions. Type specimens of *M. papillata β italica,* of *M. nepalensis,* and of *M. nitida* have all been available for study. The first and third are in good condition and show close agreement with each other and with the abundant material of *M. paleacea* from other localities. The type specimen of *M. nepalensis* bears very immature female receptacles, but the thallus characters are those of *M. paleacea* and there seems to be no reason for attempting to maintain the species as valid. Two other species quoted above among the synonyms of *M. paleacea* remain to be considered. The first of these is *M. squamosa.* Wallich's specimens of this species are clearly the same as *M. paleacea,* and since these specimens are the ones first quoted by Lehmann and Lindenberg, they might logically be considered the type. It is probable, however, that Raddi originally gave the name *M. squamosa* to his own Brazilian specimens, and this is apparently the view held by Stephani who quotes only the specimens from Brazil. Raddi's specimens have not been seen by the writer. If they should prove distinct from *M. paleacea* it might still be possible to maintain *M. squamosa* as valid. It is unfortunate that Raddi published nothing on his species himself. The second species to be considered is *M. planipora,* which the writer knows from a portion of the type material and from specimens sent by Professor Miyake. These specimens agree with *M. paleacea,* and the descriptions given by Stephani bring out no essential differences.

There is usually little difficulty in distinguishing *M. paleacea* even in the absence of receptacles. At the present time it is the only known North American species in which the epidermal pores constantly conform to the cruciate type. In this respect it agrees with *M. Berteroana* of the Southern Hemisphere, a much larger plant with very different scale-appendages and terete rays on the female receptacle. Aside from the cruciate pores *M. paleacea*

[30] Lotos 49 : 92. 1901.

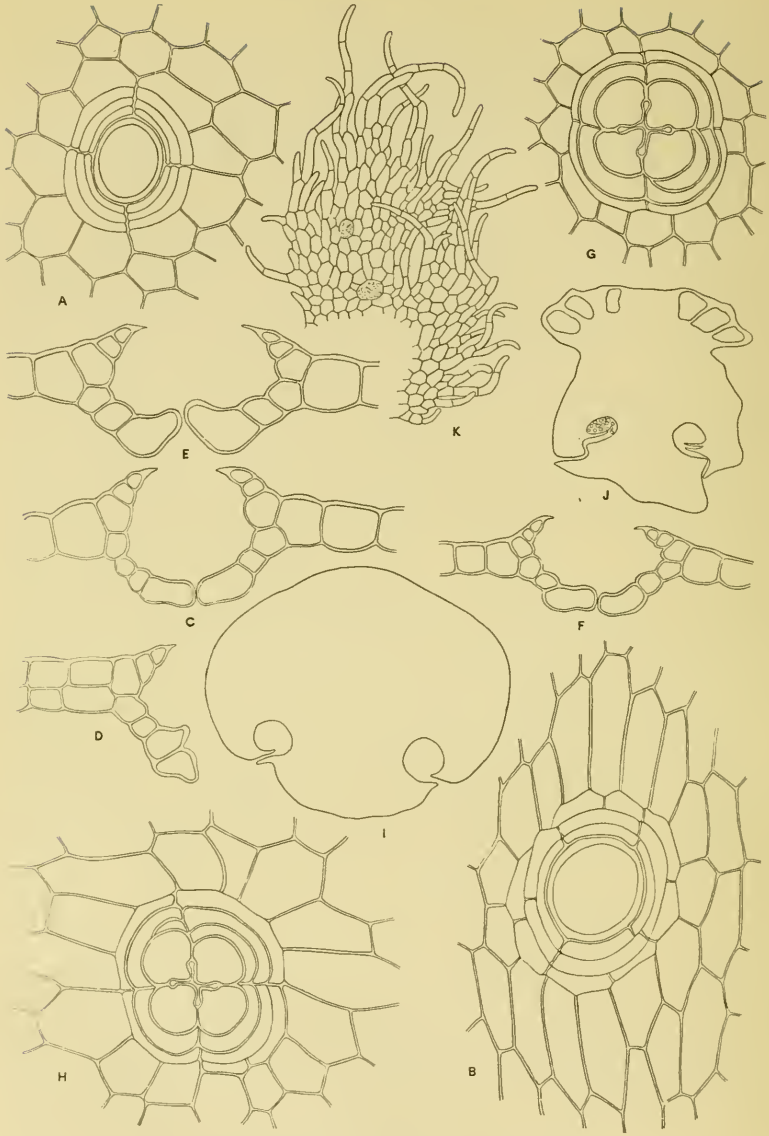

Fig. 8. Marchantia paleacea Bertol.

Anatomical details. A, B. Epidermal pores of thallus, surface view, x 225. C-F. Pores in cross-section; C, D, F, x 225; E, x 300. G, H. Pores, inner view, x 225. I. Stalk of male receptacle, cross-section, x 40. J. Stalk of female receptacle, cross-section, x 40. K. Part of involucre, x 50. A, C, D, G, J, K. Italy, *F. A. Artaria,* in V. Schiffner's Hep. Europ. Exsic. *13.* B, E, H. Vera Cruz, *Barnes & Land 668.* F. Java, *V. Schiffner,* in Iter Ind. *59,* as *M. nitida.* I. Puebla, *Frère Arsène.*

is distinguished from *M. polymorpha* by its somewhat smaller size, by its total lack of epidermal papillae, by having the pores bounded by six or seven rows of cells, by the presence of sclerotic cells, by the flattened rays of the female receptacles, by the lack of marginal scales and by marked differences in the appendages of the median scales. In *M. polymorpha* epidermal papillae are always present on cupules and female receptacles, the pores are surrounded by only four or five rows of cells, there are no sclerotic cells, the rays of the female receptacle are terete, and marginal scales are always present.

The features of the appendages in *M. paleacea* deserve particular attention (Fig. 7, B-L). When a long series is examined, it will be seen that they exhibit marked differences in their apices and margins, although they are almost constantly longer than broad and maintain an oblong or ovate form. The apex is sometimes rounded, sometimes truncate, and sometimes apiculate or even acute, while the margin may be entire throughout, variously toothed, or even provided with a basal lobe. A tooth, on its part, may be the slightest and vaguest projection of a marginal cell, it may be a distinctly projecting cell, or it may consist of a cell borne on a stalk-cell; in some of the broader teeth two adjoining cells may even be involved. It must be admitted, however, that large and complicated teeth are the exception. In commenting on the type specimen of *M. nitida* Schiffner states that the appendages are broadly ovate, less pointed at the apex and scarcely toothed, those of his Javan material being broadly cordate, abruptly pointed and with irregular and distant marginal teeth. These differences, which he considers of little importance, are shown by Fig. 7, J, L, and at first sight are somewhat striking. Since, however, equally extreme conditions are sometimes found on a single specimen, as shown by Fig. 7, G, H, it is evident that Schiffner did not underrate their value. The appendages also vary in the number of cells with oil-bodies which they show. In some cases no such cells are present; in one case as many as ten were counted; in the majority of cases there are from one to three. The gradual decrease in size between the median cells and the marginal cells is usually evident, although the actual measurements are not very different, and a distinct margin is never apparent as in *M. Berteroana*. It may be noted that Stephani assigns smaller mar-

ginal cells to *M. nepalensis, M. nitida,* and *M. tholophora,* while he states that the cells of *M. paleacea* are subequal in size, a specific difference which is not supported by actual comparisons. When contrasted with the appendages of *M. polymorpha,* those of *M. paleacea* are seen to be narrower, usually less toothed, and composed of larger cells, which show a less marked decrease in size between the median and marginal regions.

The male receptacles of *M. paleacea* seem to be infrequent. In the few cases seen the receptacles have been remarkably like those of *M. polymorpha,* although borne on shorter stalks. In other words the disc has been shortly eight-lobed with rounded rays and narrow sinuses. According to Schiffner the rays as they grow older become longer and give the disc a palmate appearance. If this is true the male receptacles exhibit a considerable range of variation. The cupules of *M. paleacea,* with their dentate, sharp-pointed lobes, likewise agree with those of *M. polymorpha* and its allies, except that the outer surface is free from epidermal papillae.

When well developed the female receptacle of *M. paleacea* consists of a disc with nine horizontal flat rays borne on an elongated stalk. In many cases the rays are about twenty degrees apart and present the appearance of being symmetrically disposed. Even here, however, the single plane of symmetry is marked by the sinus between the two basal rays, which is much deeper than the others. When the basal rays are separated by a sinus more than twenty degrees wide the plane of symmetry is more apparent and the disc does not show a radial appearance. Since the width of the sinus between the basal rays varies markedly it should not be made the basis for specific separations, although this has evidently been done in the past. The extremities of the rays are variously dilated and are truncate or even emarginate at the apex. In the center of the disc the hemispherical or bluntly conical protuberance is usually distinct, and the same thing is true of the nine rounded ridges extending from the protuberance to the beginnings of the rays. When the receptacle is young or, in some cases, when fertilization has not taken place, the rays do not spread horizontally but extend downward, and usually, under these circumstances, the median protuberance and the radiating ridges are only slightly developed. In fact they are not always distinct even when the rays have assumed

a horizontal position. Although the normal number of rays in *M. paleacea* is nine, just as in *M. polymorpha,* deviations from this number sometimes occur, a reduced number being associated with poor development.

According to Prescher scattered slime cells of small size are present in the walls of the cupules of *M. paleacea* but are lacking altogether in the thallus and in the female receptacles. Although the thallus sometimes agrees with his account it does not always do so. Cases have been observed in which slime cells formed a rather conspicuous feature of the ventral tissue of the wings, an occasional cell of this character being present even in the thickened median region. In other cases, the slime cells were less abundant. In the male receptacles, which Prescher did not examine, slime cells are fairly numerous. It is evident from these observations that the presence or absence of slime cells can not be utilized in distinguishing *M. paleacea.*

5. **Marchantia breviloba** sp. nov.

Thallus pale green, more or less glaucous, sometimes a little pigmented with purple, especially near the margin and on the lower surface, mostly 0.5-0.8 cm. wide and 2-5 cm. long, repeatedly dichotomous, the successive forks usually 1-2 cm. apart, texture firm but not leathery, margin entire; epidermis composed of cells with somewhat thickened walls, sometimes in two layers mostly 45-90μ long (averaging about 65μ) and 20-40μ wide (averaging about 28μ), papillae absent; pores (with their surrounding cells) mostly 125-150μ long and 100-120μ wide, surrounded usually by six (or seven) rows of cells (three in each series or sometimes four in the outer series), innermost row of upper series usually composed of four cells, second row of four to eight cells and third row of eight or more cells, each row of lower series usually composed of four cells, inner opening usually four-sided (sometimes three-, five-, or six-sided), the sides being concave and forming acute angles with one another, bounding cells of pore more or less roughened with a resinous deposit; air-chambers usually high, more or less elongated, their outlines very indistinct when viewed through the epidermis, present everywhere, rows of photosynthetic cells often four or five cells long; compact ventral tissue mostly twenty or twenty-five cells thick in the median portion, the walls sometimes pigmented, more or less thickened and showing distinct pits, sclerotic cells distinct, scattered, about forty in a cross-section, largely confined to median region, sometimes as much as 0.7 mm. in length, slime cells about 0.1 mm. in diameter, usually con-

spicuous (often three or four in a cross-section of thallus), scattered but more abundant toward the margin, sometimes present in the walls between air-chambers; ventral scales in two distinct rows, the laminar scales alternating with the median and only a little nearer the margin (a large portion of the ventral surface being free from scales); appendages of median scales ovate to orbicular, mostly 0.5-0.65 mm. long and 0.45-0.55 mm. wide, narrowed toward the rounded, obtuse, or apiculate apex, margin sinuate, sparingly and irregularly crenulate or denticulate from projecting cells, cells showing a gradual decrease in size toward the margin, median cells usually distinctly longer than broad, mostly 60-120μ long and 28-40μ wide, marginal cells mostly 30-50μ long and 18-25μ wide, irregular, the long axis usually forming an angle with the margin, rarely parallel with it, cells containing oil-bodies lacking: male receptacle borne on a stalk 1.5-2 cm. high, with two to four rhizoid-furrows and a single narrow dorsal band of air-chambers, the disc mostly 1-1.5 cm. broad, deeply six- (or seven-) lobed, the lobes or rays palmately disposed (the basal sinus being almost a straight line), mostly 2-5 mm. long and 1.5 mm. wide, rounded and with a thin wavy margin, ventral scales imbricated, mostly in two rows: female receptacle borne on a stalk 6-8 cm. long, with four rhizoid-furrows (except close to the base) and a single broad dorsal band of air-chambers, the disc mostly 0.6-0.8 cm. broad, usually eleven-lobed, sometimes seven- to nine-lobed, the lobes or rays short, 1 mm. long or less, flat, scarcely or not at all dilated at the truncate apex, basal sinus considerably broader than the others, upper surface of disc plane or with low ridges corresponding with the lobes; involucre ciliate, not lobed; spores yellowish brown, about 34μ in diameter, with a hyaline margin about 4μ wide, outer face bearing a few low lamellae, sometimes forming a very indistinct reticulum; elaters about 8μ wide, bispiral: cupules shortly and irregularly ciliate-dentate, the teeth sometimes adjoining and sometimes separated by sinuses of varying width, mostly two or three cells long and one or two cells wide at the base, epidermal papillae lacking. (Fig. 9.)

The following specimens of this species, which seems to be very local, have been examined:

Jamaica: without definite localities or dates, *Wilds* (N. Y., four specimens); Hardware Gap and vicinity, April, 1903, *W. R. Maxon 1115* (U. S., Y.); July, 1903, *A. W. Evans 175, 203* (Y.); Chestervale, July, 1903, *A. W. Evans 211* (Y.); vicinity of Cinchona, March, 1905, *C. E. Cummings 28* (N. Y., Y.); St. Catherine's Peak and vicinity, August, 1906, *A. W. Evans 441* (Y.). The specimens collected by Wilds include both

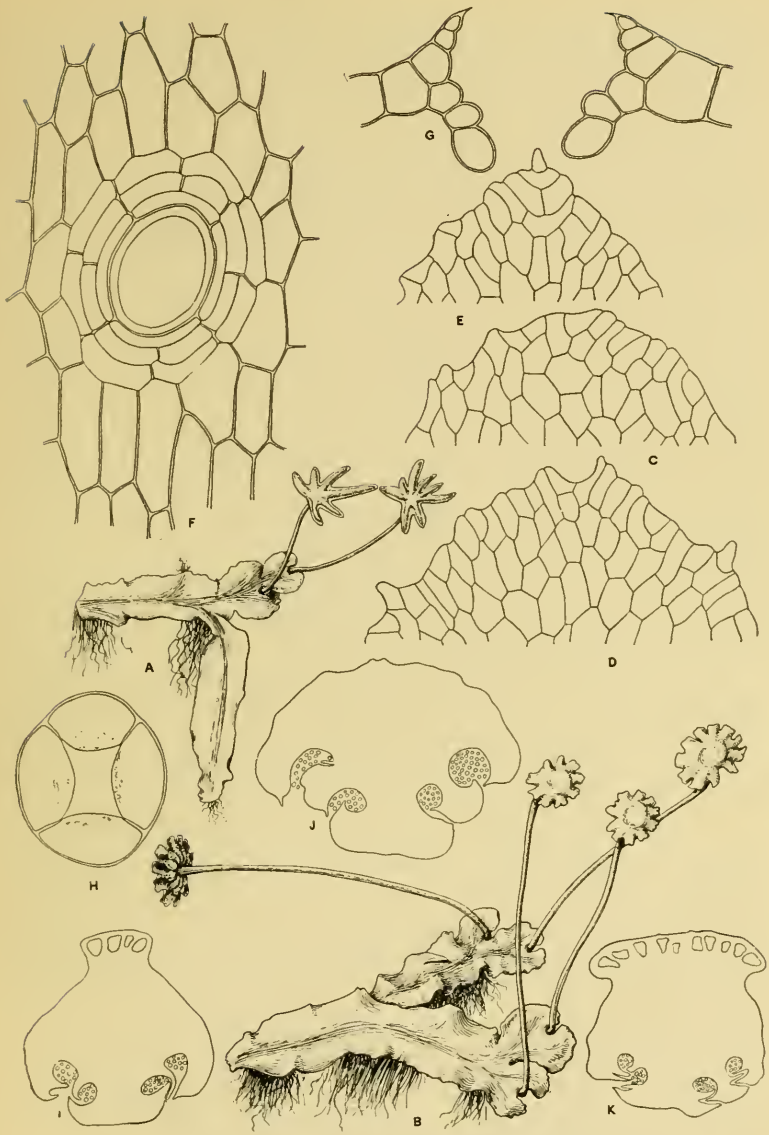

FIG. 9. MARCHANTIA BREVILOBA Evans

Plants, natural size, and various anatomical details. A. Male plant, x 1. B. Female plant, x 1. C-E. Appendages of ventral scales, apical portions, x 100. F. Epidermal pore of thallus, surface view, x 225. G. Pore in cross-section, x 225. H. Inner opening of pore, x 225. I, J. Stalk of male receptacle, cross-sections, x 40; I was cut near base; J, near apex. K. Stalk of female receptacle, cross-section, cut near base. A. Jamaica, *W. R. Maxon 1115.* B-D, F-K. Jamaica, *A. W. Evans 175,* type. E. Jamaica, *A. W. Evans, 203.*

female and gemmiparous material. Two, bearing the numbers 5 and 6, are labeled *"Marchantia conica";* the other two bear no name. No. 175, collected by the writer, may be designated the type.

The thallus of *M. breviloba* bears a strong resemblance to that of *M. paleacea,* being of about the same size and similarly subject to pigmentation. The ventral scales and the appendages of the median scales in these two species likewise have certain features in common. The arrangement of the scales, for example, is very similar and the appendages agree in form, in the gradual decrease in the size of the cells in passing toward the margin, and in some of the peculiarities of the margin itself. Even the pores look a good deal alike when examined through a lens. A detailed examination, however, quickly brings out points of difference. In *M. breviloba* the pores are not of the cruciate type, the inner opening (so far as observed) being surrounded by evenly bulging cells and thus usually exhibiting a four-sided outline with concave sides and narrow angles; in *M. paleacea* the pores are distinctly cruciate. In *M. breviloba* the cells of the appendages are markedly larger than in *M. paleacea* and oil-containing cells seem to be constantly absent; in *M. paleacea* oil-containing cells can often be detected. In *M. breviloba* slime cells seem always to be numerous and conspicuous; in *M. paleacea* they are less frequent and may be absent altogether: this last difference, unfortunately, is one to be used with caution.

The differential characters yielded by the receptacles and cupules, in separating *M. breviloba* from *M. paleacea,* are even more marked than those derived from the thallus. In *M. breviloba* the male receptacle is borne on a long stalk with a distinct band of air-chambers and usually with four rhizoid-furrows; and the disc is unsymmetrically divided into six or seven elongated lobes, the basal sinus being much broader than the others and often approximating a straight line. In *M. paleacea* the male receptacle is borne on a very short stalk without air-chambers and with only two rhizoid-furrows; while the disc is very shortly and apparently radially divided into eight (or more) often indistinct lobes, the basal sinus being of about the same width as the others.

In *M. breviloba* the stalk of the female receptacle shows four rhizoid-furrows, and the disc is very shortly lobed, the lobes

being usually more than nine and scarcely if at all dilated at the apex. In *M. paleacea* the stalk of the female receptacle shows only two rhizoid-furrows, and the disc is more deeply divided, the lobes being usually nine (or fewer) and more or less distinctly dilated at the apex; the upper surface of the disc, moreover, shows a median protuberance and nine ridges corresponding with the rays, these structures being very indistinct in *M. breviloba* or absent altogether. In *M. breviloba* the cupule is simply short-ciliate; in *M. paleacea* it shows a series of ciliate or dentate lobes.

There is no difficulty in separating *M. breviloba* from *M. polymorpha.* The new species is smaller, it lacks marginal ventral scales, the appendages of the median scales have larger cells and usually fewer marginal teeth, the epidermal cells are more complex being surrounded by more rows of cells, there are no epidermal papillae, the stalk of the male receptacle has air-chambers and usually more rhizoid-furrows, the disc is more deeply and more unsymmetrically lobed, the stalk of the female receptacle has more rhizoid-furrows, the disc is less deeply lobed, and the lobes are flattened instead of being terete. The difference in the cupules, already noted in connection with *M. paleacea,* would apply equally well in separating the species from *M. polymorpha.*

6. Marchantia domingensis Lehm. & Lindenb.

Marchantia domingensis Lehm. & Lindenb.; Lehmann, Pug. Plant. 6: 22. 1834.
Marchantia inflexa Nees & Mont.; Montagne, Ann. Sci. Nat. Bot. II. 9: 43. 1838.
Marchantia disjuncta Sulliv. Am. Jour. Sci. II. 1: 74. 1846.
Marchantia linearis G. L. & N. Syn. Hep. 529. 1847 (in part). Not Lehm. & Lindenb.
Marchantia martinicensis Spreng.; G. L. N. *l. c.* 531. 1847 (as synonym).
Marchantia Elliottii Steph. Bull. Herb. Boissier 7: 400. 1899.
Marchantia caracensis Steph. *l. c.* 526. 1899.

Thallus pale to dark green, not glaucous, slightly or not at all pigmented with purple, usually 4-6 mm. wide and 2-3 cm. long, dichotomous, the successive forks usually 1-1.5 cm. apart, texture delicate, margin entire; epidermis composed of cells with

slightly thickened walls, sometimes in two layers, mostly 30-60μ long (averaging about 45μ) and 15-30μ wide (averaging about 23μ), papillae absent; pores (with their surrounding cells) mostly 90-130μ long and 70-80μ wide, surrounded usually by six (or seven) rows of cells (three or four in the upper and three in the lower series), the two lower rows of the upper series usually composed of eight (six to ten) cells apiece (more rarely of only three to five cells), the other rows of four (three to five) cells apiece, inner opening usually four-sided, more rarely three- or five-sided, with the sides straight or nearly so, the bounding cells more or less obscured by a resinous deposit; air-chambers of medium height, isodiametric or somewhat elongated, their boundaries sometimes distinct and sometimes vague when viewed through the epidermis, present everywhere, rows of photosynthetic cells often four or five cells long but sometimes shorter; compact ventral tissue about twenty cells thick in the median portion, the walls sometimes pigmented, more or less thickened and showing distinct pits, sclerotic cells usually distinct, scattered, mostly five to thirty in a cross-section, more abundant in the median portion but sometimes present in the wings, in the latter case often distinctly visible without sectioning, slime-cells lacking; ventral scales in two distinct rows, the laminar scales alternating with the median scales and not much nearer the margin; appendages of the median scales broadly lanceolate to ovate, when well developed mostly 0.35-0.6 mm. long and 0.27-0.45 mm. wide but sometimes considerably smaller, apex apiculate, acute, or cuspidate, margin more or less densely denticulate or dentate, the teeth usually one or two cells long, cells showing a gradual and slight decrease in size toward the margin, median cells usually longer than broad, mostly 40-80μ long and 20-40μ wide, marginal cells mostly 20-40μ long and 15-20μ wide, irregular but the long axis usually at right angles or nearly so to the margin, cells containing oil-bodies apparently always lacking: male receptacle borne on a stalk 5 mm. long or less, with two to four rhizoid-furrows and a single broad dorsal band of air-chambers, the disc variable in size but mostly 6-8 mm. broad, deeply lobed, the lobes or rays usually four to six but sometimes two, three, seven or eight, palmately disposed, the basal sinus a very broad angle or a straight line, mostly 3-6 mm. long and 2-3 mm. wide, rounded, with a thin wavy margin extending across the basal sinus, ventral scales imbricated, in two or more rows; female receptacle borne on a stalk 1.5-2 cm. high, with two to four rhizoid-furrows and a single broad dorsal band of air-chambers, the disc mostly 5-7 mm. wide, the lobes or rays spreading at maturity, extending about half way from the margin to the center, normally seven but often only five or six, more rarely eight to eleven, slightly or not at all dilated at the truncate, irregularly crenate or slightly emarginate apex, upper

surface of disc and rays usually plane but sometimes more or less convex, basal sinus broader than the others and sometimes forming a very obtuse angle; involucre very delicate, the margin minutely and often irregularly crenulate to short-ciliate, the teeth usually varying from one to three cells in length; spores brownish yellow, about 28μ in diameter, the outer face bearing a series of low irregular ridges not forming a network; elaters about 6μ wide, bispiral: cupules closely short-ciliate, the cilia mostly one to four cells long, outer surface without papillae. (Figs. 10-12.)

A widely distributed species in the southern United States, the West Indies, Mexico, Central America, and Venezuela. The following specimens have been examined:

Tennessee: Etowah, June, 1909, *F. McCormick* (C. C. H., Y., listed as *M. disjuncta* by the writer in Bryologist 13:33. 1910).

Georgia: west bank of Ocmulgee River, Hawkinsville, June, 1902, *R. M. Harper 1382a* (N. Y., U. S.); Samochechobee Creek, near Killen, Clay County, October, 1902, *R. M. Harper 1791b* (N. Y., U. S.); Flint River swamp, below Albany, Dougherty County, August, 1903, *R. M. Harper 1951e* (N. Y., U. S.).

Florida: Devil's Millhopper, Alachua County, February, 1909, *R. M. Harper 14* (N. Y.); April, 1915, *N. L. T. Nelson 45, 46, 47, 51* (Y.).

Alabama: banks of the Alabama River near Claiborne, *W. S. Sullivant* (H., type locality of *M. disjuncta,* specimens distributed in Musc. Alleg. *286* and Hep. Bor.-Amer. *128*); Auburn, May, 1896, *L. M. Underwood* (N. Y., Y., distributed, as *M. disjuncta,* in Hep. Amer. *182*); June, 1897, *Earle & Baker 52* (N. Y.).

Texas: Fort Worth, 1887, *G. S. Thompson 10* (N. Y., U. S., listed as *M. disjuncta* by Underwood in Bot. Gaz. 20:69. 1895); Hallettsville, May, 1892, *G. C. Nealley 59* (C. C. H., U. S.); Austin, March, 1909, *F. D. Heald* (Y.).

Arkansas: Fort Harvey, no date, *F. L. Harvey 2* (N. Y., listed as *M. disjuncta* by Underwood, *l. c.*).

Mexico: without definite locality or date, *C. H. Schultz 1229* (B., listed as *M. papillata,* by Stephani in Bull. Herb. Boissier 7:397. 1899).

Hidalgo: Tula, *C. G. Pringle 10675* (Y., distributed in Pl. Mex. under a manuscript name of Stephani).

Puebla: banks along Avenida Hidalgo and path to barranca, Tezuitlan, 1908, *Barnes & Land 553* (Y.).

Tamaulipas: near Victoria, June, 1907, *E. Palmer 446* (N. Y., Y.).

Vera Cruz: Orizaba and vicinity, 1855, *F. Müller 2373* (N. Y., listed as *M. disjuncta* by Underwood, *l. c.*); 1857, *C. Mohr* (N. Y., Y.); March, 1890, *W. Stone 114, 115* (N. Y., listed by Underwood, *l. c.*); 1892, *J. G. Smith* (N. Y., Y.); Cordova, 1885, *W. G. Farlow 18* (N. Y., listed as *M. tholophora* by Underwood, *l. c.* 70).

Guatemala: Black River, *S. Watson 295b* (H., N. Y., listed as *M. linearis* by Underwood, *l. c.* 69); near the Finca Sepacuite, Alta Verapaz, March and April, 1902, *Cook & Griggs 82, 255, 403* (U. S., Y.).

Bahamas: Fort Charlotte, New Providence, April, 1905, *L. J. K. Brace 3916* (N. Y., Y., listed as *M. chenopoda* by the writer in Bull. Torrey Club 38: 206. 1911); New Providence, October, 1904, *L. J. K. Brace 873* (N. Y.).

Cuba: without definite localities or dates, *C. Wright* (distributed as *M. disjuncta* and *M. linearis* in Hep. Cubenses); San Andre, April 14, 1865, *C. Wright* (H., Y.); valley of the San Juan River, near Matanzas, March, 1903, *Britton, Britton & Shafer 326* (N. Y., Y.); Guines, Havana, March, 1905, *M. T. Cook* (N. Y., Y.); Almendares River, near Puentas Grandes, Havana, April, 1908, *Brother Leon 723* (N. Y., Y.); falls of the Habanilla and near Siguanea, Trinidad Mountains, Santa Clara, March, 1910, *E. G. Britton 4855, 5076* (N. Y., Y.); vicinity of Guane, Pinar del Rio, March, 1911, *Britton, Britton & Cowell 9770* (N. Y., Y.); vicinity of Pinar del Rio, March, 1911, *E. G. Britton 10017* (N. Y., Y.); Finca Guerrero, Rio Yayabo, St. Spiritus, Santa Clara, December, 1911, *Brother Clement 44* (N. Y., Y.); Banaos Hills, Santa Clara, August, 1913, *Brother Leon 4036* (N. Y., Y.); Ensenada de Mora, Oriente, March, 1912, *Britton, Cowell & Shafer 13005* (N. Y., Y.).

Santo Domingo: Azui, province of Seibo, November, 1909, *N. Taylor 281* (N. Y., Y.).

Jamaica: without definite locality or date, *N. Wilson 595, 611* (N. Y., listed as *M. disjuncta* by Underwood, *l. c.*); Hartford and adjoining properties, near Priestman's River, June,

1904, *W. R. Maxon 2535* (U. S., Y.); road from Holly Mount to Resource, February, 1905, *W. Harris 8876* (N. Y., Y.); vicinity of Mandeville, September, 1907, *E. G. Britton 429* (N. Y., Y.); February, 1910, *S. Brown 280, 282, 283* (N. Y., Y.); Kempsport and Roaring River Falls, March, 1908, *E. G. Britton 668, 708* (N. Y., Y.); Porus to Clarendon Park, September, 1908, *N. L. Britton 3785* (N. Y., Y.); Cokely, near Castleton, and Hope Gardens, January, 1914, *W. Harris* (N. Y.).

Porto Rico: Las Marias Road and vicinity of Mayaguez, March, 1906, *Britton & Marble 594, 613* (N. Y., Y.); Lares to San Sebastiano, April, 1913, *Britton & Marble 2797, 2803* (N. Y., Y.); Rio de Maricao, April, 1913, *E. G. Britton 2494* (N. Y., Y.); Ciales, August, 1913, *J. R. Johnston 940* (N. Y., Y.); between Arecibo and Utuado, July, 1901, *Underwood & Griggs 836* (U. S., Y.); March, 1914, *E. G. Britton 2074* (N. Y., Y.); Lares, June, 1901, *Underwood & Griggs 36* (U. S., Y.); June, 1914, *J. R. Johnston 2070* (N. Y., Y.); Monte Montoso, February, 1915, *Britton & Cowell 4177* (N. Y., Y.); La Juanita, near Las Marias, February, 1915, *E. G. Britton 3965* (N. Y., Y.); vicinity of Utuado, March, 1915, *E. G. Britton 5168, 5112* (N. Y., Y.).

St. Kitts: Bethesda, *J. C. Breutel* (N. Y., listed as *M. linearis* in Syn. Hep. 529 and as *M. domingensis* by Stephani in Bull. Herb. Boissier 7: 399. 1899); without definite locality, 1853, *Walwyn* (N. Y.); Old Road and Lambert Estate, September and October, 1901, *Britton & Cowell 481, 626* (N. Y., U. S., Y.).

Montserrat: mountain pass to Roches and Tar River, February, 1907, *J. A. Shafer 867, 871* (N. Y., Y.).

Guadeloupe: Morne Rouge, Gombeyre (Basse-Terre) and Morne Papillon, 1897-1900, *Père Duss 250, 251, 312, 392* (N. Y., Basse-Terre specimens listed as *M. disjuncta* by Schiffner in Oesterr. Bot. Zeitschr. 57: 51. 1907).

Dominica: without definite locality or date, *W. R. Elliott 1292* (B., type of *M. Elliottii*).

Martinique: without definite locality, date, or collector's name (M., received from Mérat, type of *M. inflexa*); without definite locality or date, *Sieber 378* (N. Y., probably type of *M. martinicensis*); St. Pierre and between Deux-Choux and Gros-Morne, 1899, 1900, *Père Duss 342, 393* (N. Y.); Morne Rouge,

August, 1901, *Père Duss 578, 580, 581* (N. Y.); Deux-Choux, September, 1903, *Père Duss* (N. Y., determined as *M. caracensis* by Stephani).

St. Vincent: without definite localities or dates, *L. Guilding* (H., N. Y., specimens in the Taylor and Mitten herbaria, labeled *"March. linearis—chenopoda."*):

Grenada: Annandale, St. George's, March, 1906, *W. E. Broadway* (N. Y.).

Trinidad: without definite locality, 1878-80, *A. Fendler* (N. Y., U. S., Y., distributed as *M. chenopoda*); Mareval Valley, 1913, *R. Thaxter* (H., Y.); La Lenia Valley, 1913, *R. Thaxter* (H., Y.).

Venezuela: Rio Cartude, Caracas, 1856, *Gollmer* (B., type of *M. caracensis*); Caracas, August, 1902, *A. F. Blakeslee.* (H., Y.).

The following stations, cited in literature, should also be noted:

Santo Domingo: without definite locality, date or collector's name (type).

Guadeloupe: without definite locality or date, *L'Herminier 69* (listed, as *M. linearis,* by Bescherelle in Jour. de Bot. 7: 193. 1893).

Martinique: without definite localities or dates, *C. Bélanger 124* (listed, as *M. linearis,* by Bescherelle, *l. c.*); *K. von Martius; C. Bélanger 24* in part, *374; Hahn 774* (the last three listed, as *M. inflexa,* by Bescherelle, *l. c.*).

The type specimen of *M. domingensis* was collected in Santo Domingo, neither the date nor the collector's name being mentioned in the original publication. Unfortunately this specimen has not been available for study. In its absence the writer has been obliged to rely upon West Indian material determined as *M. linearis* and upon the type specimen of *M. inflexa.* These are referred to *M. domingensis* without question by Stephani and agree in all essential respects with the other specimens listed. The type specimens of *M. disjuncta, M. Elliottii* and *M. caracensis* have likewise been examined and show a similar agreement. The writer feels convinced, therefore, that the synonymy given above is correct.

The type specimen of *M. inflexa,* received from the Montagne herbarium, is very fragmentary but bears two female recep-

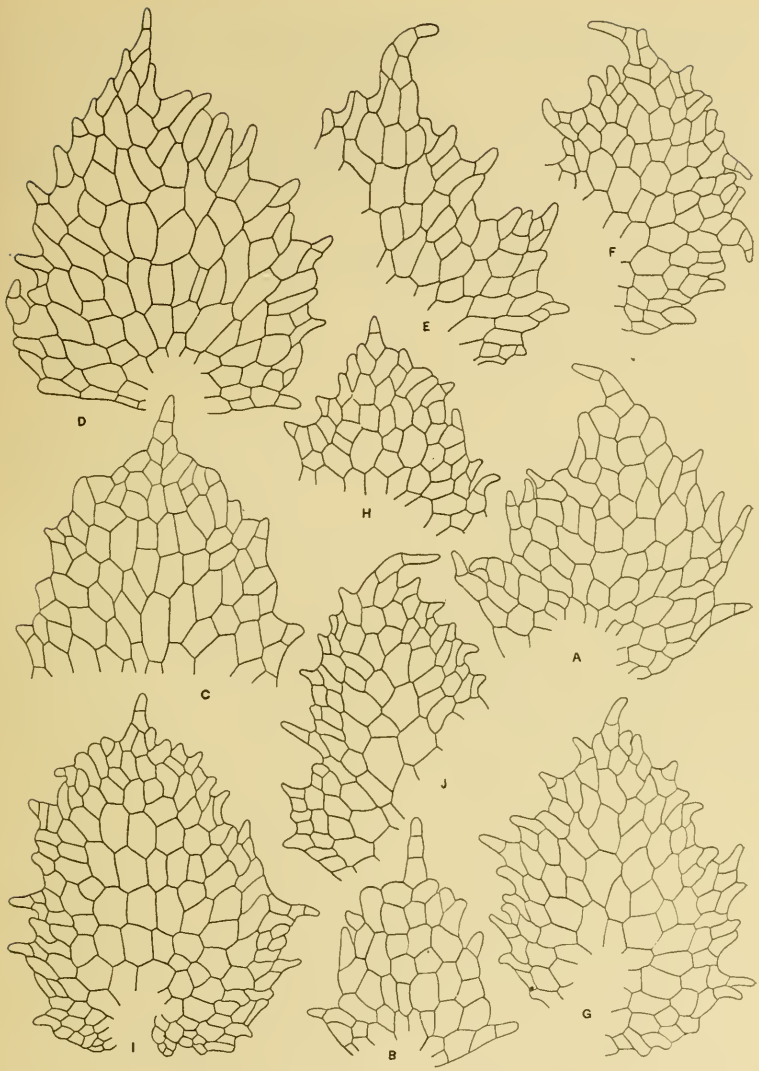

FIG. 10. MARCHANTIA DOMINGENSIS Lehm. & Lindenb.

Appendages of ventral scales, x 100. A, B. Alabama, *Earle & Baker 52*. C. Cuba, *C. Wright,* distributed in Hep. Cubenses, as *M. disjuncta*. D, E. Hope Gardens, Jamaica, *W. Harris*. F. St. Kitts, *J. C. Breutel,* specimen in the Mitten herbarium, labeled *M. linearis* and *M. chenopoda*. G. St. Kitts, *Britton & Cowell, 626*. H. Martinique, type of *M. inflexa*. I, J. Mareval Valley, Trinidad, *R. Thaxter*.

tacles: the first shows nine truncate rays clearly, the basal sinus being broader than the others; the second shows ten less clearly marked rays. The type of *M. disjuncta* agrees closely with the specimens distributed by Sullivant, by Austin, and by Underwood. They are well represented in the beautiful figures published by Sullivant,[31] and the female receptacles show a variable number of rays. The type of *M. Elliottii* bears numerous female receptacles, which show from five to nine rays apiece, the rays being plane or slightly convex and blunt. The type of *M. caracensis* bears both cupules and female receptacles, the latter showing five rays apiece. All of these specimens show the dentate scale appendages and other features characteristic of the species.

The thallus of *M. domingensis* is smaller and usually more delicate in texture than in any of the preceding species. In wet localities the photosynthetic layer is especially thin and the epidermis is rarely more than a single cell in thickness, so that plants growing under these conditions present an unusually fragile aspect. The epidermal pores, however, maintain their complex structure and form conspicuous whitish dots on the upper surface. Sometimes the boundaries of the air-chambers show distinctly through the epidermis, but they are usually indistinct. The structure of the pores is much the same as in *M. breviloba,* although the inner opening is bounded by straighter lines.

The sclerotic cells in the thallus exhibit a great deal of variability. When abundantly developed they occur both in the thickened median portion of the thallus and in the wings, those in the latter position showing distinctly as elongated brown spots when examined from underneath. The sclerotic cells appear to be separated from one another by parenchyma when a cross section of a thallus is examined. As a matter of fact, in the median portion of the thallus at least, they often form elongated strands running for a considerable distance, the acute ends of the cells slightly overlapping. There are many cases, however, where the sclerotic cells are very scantily developed. Sometimes there are none at all present in the wings although the median portion still retains them; sometimes even the median portion seems to

[31] Mem. Am. Acad. II. 3: *pl. 3.* 1846.

lack them completely, although no specimens have yet been seen in which a careful examination failed to show traces of sclerotic cells in this region.

The appendages of the ventral scales (Fig. 10) have better developed teeth than in any other North American species of *Marchantia,* although the South American *M. papillata* is a close

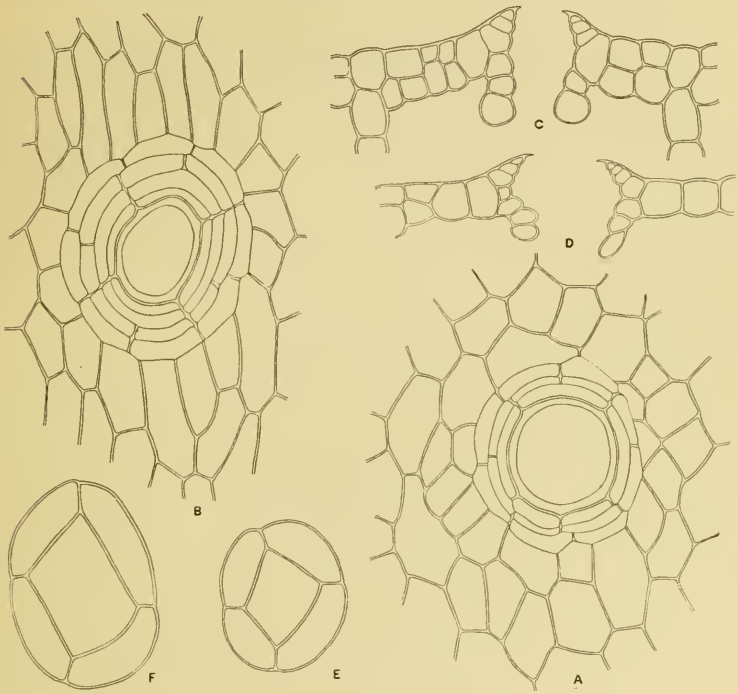

Fig. 11. Marchantia domingensis Lehm. & Lindenb.

Epidermal pores of thallus, x 225. A, B. In surface view. C, D. In cross-section. E, F. Inner openings. A, C, E. Texas, *F. D. Heald.* B, D, F. Cokely, near Castleton, Jamaica, *W. Harris.*

rival in this respect. The teeth are very irregular, the simplest being single cells which project as rounded or bluntly pointed processes. Between these simple teeth and irregular lobes, several cells long and wide, are all possible gradations. The apical tooth tends to be longer than the others, although this tendency is not always apparent. The median cells of the appendages are often longer than broad and a decrease in the size of the cells

between the middle portion and the margin is distinctly evident. There is no definite border, however, as in *M. Berteroana.* Sometimes, in wet situations, the appendages remain very small, although even under these circumstances the marginal teeth form a conspicuous feature. The more sharply pointed apices, the larger and more irregular teeth, the larger marginal cells and the lack of cells containing oil-bodies will at once distinguish the appendages of *M. domingensis* from those of *M. polymorpha.*

According to the original description of *M. domingensis* the female receptacle is semicircular and ten-lobed to the middle, the lobes being dilated and emarginate-crenate at the apex. The Synopsis gives the number of lobes as seven to ten, while Stephani states that nine lobes are present. The original description of *M. inflexa* assigns nine to eleven lobes to the receptacle, while Sullivant gives seven to nine as the number of lobes in *M. disjuncta;* here again Stephani places the number of lobes definitely at nine, and gives the same number for *M. Elliottii.* In *M. caracensis,* however, he states that only five or six lobes are present. As a matter of fact the receptacles are exceedingly variable and it is not easy to decide what the typical or normal number of lobes really is. In the material from the mainland seven is perhaps the usual number but five lobes often occur and more than seven have been observed in several instances. In the West Indian material nine lobes are present more frequently, but seven or even only five lobes are not unusual. Sometimes the lobes seem to be subdivided, so that it is not always easy to count them except by means of the involucres which alternate with them. The lobes vary not only in number but in thickness. In some cases they are very thin and flat, in other cases thicker and convex. When the lobes are fleshy the center of the disc sometimes shows a low swelling, but it is usually plane, and the receptacle never shows the conspicuous median protuberance and radiating ridges which are so characteristic of *M. paleacea.*

The study of the involucre is beset with considerable difficulty on account of its extreme delicacy. This has apparently been the cause of considerable confusion in the published descriptions. In *M. domingensis,* for example, the involucre is said to be laciniate-ciliate or shortly fimbriate; in *M. inflexa,* laciniate; in *M. disjuncta,* sparingly dentate or subentire; in *M. caracensis,* shortly fimbriate. Fig. 12, E-J, brings out the range of variation

observed by the writer. The nearest approach to an entire condition is seen in FIG. 12, E, although even here the margin is distinctly and closely crenulate; in FIG. 12, F, the crenulate condition is more pronounced, some of the teeth being two cells long; in FIG. 12, G, a crenulate portion directly adjoins a short-ciliate portion, in which the cilia are two or three cells long; in FIG.

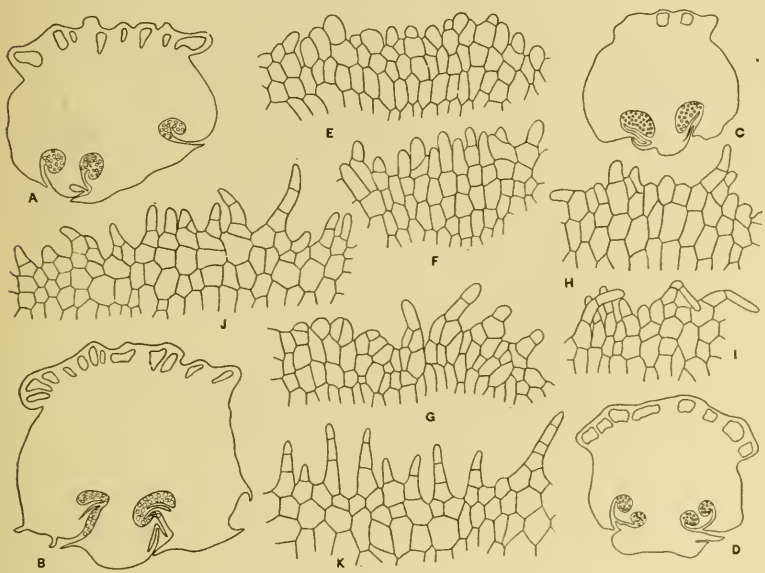

FIG. 12. MARCHANTIA DOMINGENSIS Lehm. & Lindenb.

Anatomical details. A. Stalk of male receptacle, cross-section, x 40. B-D. Stalks of female receptacles, cross-sections, x 40, C having been cut near base. E-J. Parts of involucres, x 100: H and I were dissected from a single involucre; J, from another involucre on the same receptacle. K. Part of cupule, x 100. A. Florida, *N. L. T. Nelson 47*. B, F. Texas, *F. D. Heald*. C, H-J. Jamaica, *E. G. Britton 668*. D. St. Kitts, *Britton & Cowell 626*. E. Alabama, *Earle & Baker 52*. G. Guatemala, *Cook & Griggs 82*. K. Cokely, Jamaica, *W. Harris*.

12, H-J, taken from a single receptacle, the variation to be expected is shown with especial clearness, some of the marginal teeth or cilia being straight and some curved. In all probability the laciniate and fimbriate involucres of the descriptions have been the result of irregular tears in old material.

In the case of the male receptacle, Sullivant states that the number of lobes in *M. disjuncta* is normally seven, although some

of his figures show six, four, or only three lobes. Stephani places the number at about eight in his account of *M. disjuncta* but makes no mention of the male receptacles in *M. domingensis, M. Elliottii* or *M. caracensis.* Apparently a good deal of variation is to be expected from varying environmental conditions, as Goebel[32] has recently noted, poorly developed material showing a reduced number of lobes. Even when only two rays are present the upper part of the stalk shows two rhizoid-furrows, although the lower part shows but one. The deeply lobed male receptacle will distinguish *M. domingensis* from all the preceding species except *M. breviloba.* In addition to its greater size this species differs from *M. domingensis* in the appendages of the ventral scales, which are larger and much less toothed; in the slime cells of the thallus, these structures being apparently never found in *M. domingensis;* in the less deeply lobed female receptacles; and in the distinctly ciliate involucres.

7. Marchantia papillata Raddi

Marchantia papillata α brasiliensis Raddi, Mem. Soc. Ital. Modena 19: 44. 1823; 20: *pl. 6a, f. 3, 4.* 1829.

Marchantia platycnemos Schwaegr.; Gaudichaud, Freyc. Voy. Bot. 218. 1827 (as to the Brazilian plant).

Marchantia androgyna Nees; Martius, Fl. Brasil. 1: 308. 1833. Not L.

Marchantia subandina Spruce, Trans. Bot. Soc. Edinburgh 15: 561. 1885.

Thallus dull green, not glaucous, sometimes more or less pigmented with purple, usually 1.5-3 mm. wide and 0.8-1.15 cm. long, dichotomous, the forks usually only 1.5-3 mm. apart, texture firm, margin entire; epidermis composed of cells with more or less thickened walls, usually in a single layer, mostly 20-50μ long (averaging about 30μ) and 12-20μ wide (averaging about 15μ), papillae absent; pores (with their surrounding cells) mostly 50-70μ long and 40-45μ wide, surrounded usually by five (or six) rows of cells (two or three in the upper series and three in the lower series), each row usually composed of four cells (rarely of three or five), the lowest row of the upper series sometimes with from five to eight cells, inner opening usually four-sided (rarely with three or five sides), the sides concave,

[32] Organographie der Pflanzen, 2d ed. 699. 1915.

bounding cells more or less obscured by a resinous deposit; air-chambers low, isodiametric or somewhat elongated, their outlines very indistinct when viewed through the epidermis, present everywhere, rows of photosynthetic cells usually two or three cells long; compact ventral tissue about fifteen cells thick in the median portion; the walls sometimes pigmented, more or less thickened and showing distinct pits, sclerotic cells scattered, mostly fifteen to twenty in a cross-section, more abundant in the median portion but often present in the wings, sometimes clearly visible without sectioning, slime cells lacking; ventral scales in two rows, the row of laminar scales more or less irregular but tending to alternate with the median scales and not much nearer the margin; appendages of the median scales ovate, when well developed mostly 0.3-0.45 mm. long and 0.25-0.3 mm. wide but sometimes considerably smaller, apex apiculate, acute, or cuspidate, margin subentire or usually more or less closely denticulate or dentate, the teeth irregular, mostly one or two cells long, rarely larger and more lobe-like, cells showing a gradual and slight decrease in size toward the margin, median cells usually longer than broad, mostly 49-60μ long and 25-30μ wide, marginal cells mostly 30-45μ long and 15-25μ wide, irregular but usually with the long axis at right angles or nearly so to the margin, cells containing oil-bodies apparently always lacking, male receptacle borne on a stalk about 3 mm. long with two rhizoid-furrows, the disc about 0.8 cm. wide, deeply four- to eight-lobed, the lobes or rays palmately disposed (the basal sinus being very broad), about 3 mm. long and 1 mm. wide, rounded at the apex and with a thin wavy margin, ventral scales imbricated: female receptacle borne on a stalk 1.5-2 cm. long, with two rhizoid-furrows and a single broad dorsal band of air-chambers, the disc mostly 3-4 mm. broad, normally nine-lobed (but sometimes with five to eight lobes), the lobes or rays 1-1.5 mm. long and about 1 mm. wide, distinctly dilated at the truncate to emarginate apex, strongly convex on upper surface, basal sinus broader than the others, upper surface of disc with a low median protuberance; involucre very delicate, irregularly lobed and crispate, otherwise entire or slightly and irregularly crenulate; pores yellowish brown, about 26μ in diameter, outer face bearing a series of very low ridges not forming a network, margin narrow and often indistinct, less than 2μ broad; elaters about 8μ broad, bispiral: cupules sparingly and irregularly denticulate to short-ciliate, the teeth being projections of marginal cells or from one to four cells long, epidermal papillae lacking. (Fig. 13.)

The following specimens have been examined:

Brazil: Rio de Janeiro, without date, *G. Raddi* (N. Y., type); without date, *J. Milne* (N. Y.); without definite locality or date, *W. J. Burchell 1857* (N. Y.).

Paraguay: Paraguari, August, 1883, *B. Balansa* (N. Y., U. S., distributed in Pl. du Paraguay *4006,* and listed by Stephani in Rev. Bryol. 14: 58. 1887).

Peru: near the Rio Huallaga, *R. Spruce* (type of *M. subandina,* distributed in Hepaticae Spruceanae).

Bolivia: Isapuri, October, 1901, *R. S. Williams 2145* (N. Y., Y.).

Although the writer has seen no specimens of *M. papillata* from other localities, the following records may be cited from the literature:

Cuba: "ad terram in locis humidis prope S. Marcos," *Ramon de la Sagra,* gemmiparous specimens (listed by Montagne in Ramon de la Sagra, Hist. Fis. Pol. y Natur. Cuba 9: 290. 1845).

Martinique: without definite locality or collector's name (listed by Underwood in Bot. Gaz. 20: 70. 1895); without definite locality or date, *A. Plée 1821* (listed by Bescherelle in Jour. de Bot. 7: 193. 1893).

Brazil: Rio Janeiro, *C. Gaudichaud* (listed, as *M. platycnemos,* in Freyc. Voy. Bot. 218. 1827); Minas Geraes, *K. von Martius* (listed by Nees von Esenbeck in Naturg. Europ. Leberm. 4: 109. 1838); "ad muros humidos aquaeductus, loco Corcovado dicto" near Rio de Janeiro, and "ad terram juxta flumen Rio Negro", *A. d'Orbigny* (listed by Montagne in D'Orbigny, Voy. dans l'Amér. Mérid. 7[2]: 397. 1839).

Falkland Islands: without definite locality or date, *C. Gaudichaud* (listed, as *M. platycnemos,* in Freyc. Voy. Bot. 218. 1827).

The original *M. papillata* included two varieties, *α. brasiliensis* and *β. italica.* Nees von Esenbeck[33] soon showed, however, that the second variety was a synonym of *M. paleacea;* he therefore reserved the name *M. papillata* for the first variety, a course which has been followed by subsequent writers. He was also the first to recognize the fact that his Brazilian *M. androgyna* belonged to *M. papillata* and to include *M. platycnemos* among the synonyms of the same species. It is possible, however, that *M. platycnemos* ought still to be maintained as a species, at least in part. It was based on three specimens, the first from the

[33] Naturg. Europ. Leberm. 4: 101. 1838.

Marianne Islands in the Pacific, the second from the Falkland Islands, and the third from Brazil. The first specimen may be regarded as the type of the species since it is mentioned first. A portion of this specimen in the herbarium of the New York Botanical Garden shows that the type is distinct from *M. papillata,* as here understood, but that it is very close to *M. emarginata* and perhaps synonymous with it. Nees von Esenbeck's inclusion of *M. platycnemos* among the synonyms of *M. papillata* must therefore be considered as applying to a part only of Schwaegrichen's species as originally described.

Of Raddi's original figures, *f. 3* is said to represent male plants and *f. 4,* female plants. This is obviously an error, the receptacles shown under *f. 3* being clearly female. In *f. 3a* six receptacles are drawn, two showing six lobes apiece and one seven lobes, the number being doubtful in the other three. In *f. 3b* an enlarged receptacle with nine lobes is represented; the lobes show clearly the enlarged apices with more or less distinct emarginations, and no difference is brought out between the basal sinus and the others. The receptacles shown in *f. 4* are very doubtful and bear a disc which is scarcely lobed at all. Unless drawn from very immature material they probably belong to some other species than *M. papillata.* It should be noted, however, that the Synopsis describes the disc of the male receptacle as "subdimidiato excentrico marginibus repando-lobatis," thus evidently recognizing a male receptacle in Raddi's so-called female receptacle; but Stephani apparently discards this view, since he does not mention the male receptacles at all.

The specimen of *M. papillata,* quoted above as the type, is in the Mitten herbarium and was received from Hooker. It is very fragmentary but includes three female receptacles, two showing eight lobes apiece and the third, seven lobes. The dilated apices of the lobes and the broader basal sinus are clearly apparent. This specimen has been carefully compared with the other specimens cited and found to agree with them in all essential respects. Spruce compares *M. subandina* with both *M. papillata* and *M. Berteroana,* which he knew from description only. He ascribes to the species, however, a polyoicous inflorescence and monospiral elaters. Unfortunately the specimens which he distributed, although agreeing with his description in other respects, show a strictly dioicous inflorescence and bispiral

elaters, so that his statements about the inflorescence and elaters must have been based on a misconception.

The thallus of *M. papillata* is even smaller than in *M. domingensis;* it is, in fact, the smallest American species known at the

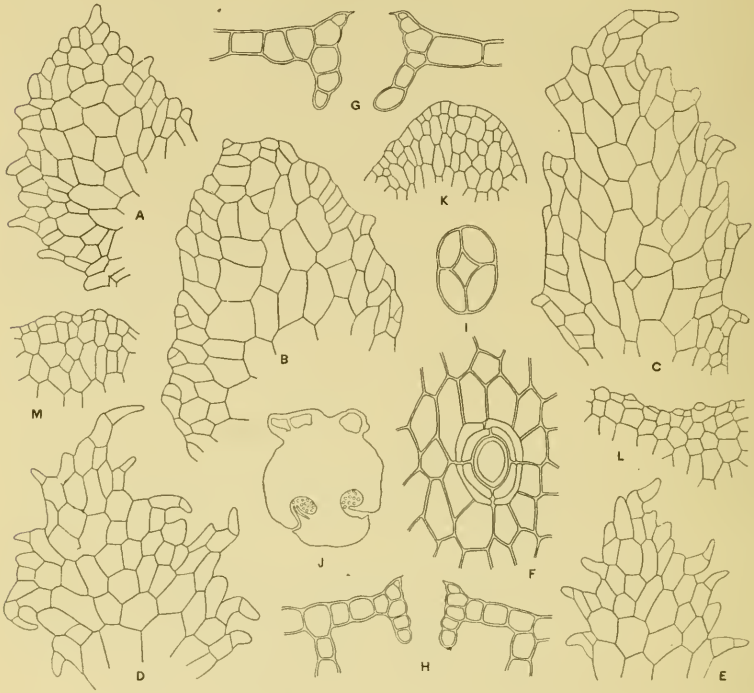

Fig. 13. Marchantia papillata Raddi

Appendages of ventral scales and other anatomical details. A-E. Appendages of ventral scales, B and C having been dissected from the same thallus, x 100. F. Epidermal pore of thallus, surface view, x 225. G, H. Pores in cross-section, x 225. I. Inner opening of pore, x 225. J. Stalk of female receptacle, cross-section, x 40. K-M. Parts of involucres, x 100. A. Brazil, *G. Raddi,* type. B, C, G, J, K. Paraguay, *B. Balansa 4006.* D-F, H, I. Bolivia, *R. S. Williams 2145.* L, M. Peru, *R. Spruce,* type of *M. subandina.*

present time. So far as the structure of the thallus is concerned the agreement with *M. domingensis* is very close. Slime cells seem to be always lacking in both species and sclerotic cells are usually abundant and equally conspicuous. The appendages of the median scales, moreover, are essentially the same, although the marginal teeth in *M. papillata* exhibit a slightly wider range

of variability. There are, however, certain differences in the epidermal cells and pores which deserve some emphasis. The cells and pores are not only distinctly smaller than in *M. domingensis,* but the pores are constructed on a simpler plan, the opening being surrounded by fewer rows of cells and the number of cells in each row being less subject to variation. The cells bounding the inner opening tend to be more convex. It must be admitted that these differences are very slight and might not deserve much attention if they were not supported by other differences derived from the female receptacle.

The variability of the receptacles with respect to the number of lobes has already been commented upon in connection with the type specimen and becomes still more apparent from a study of the published descriptions. According to Nees von Esenbeck the usual number of lobes is seven, eight to ten being sometimes present; according to Spruce nine lobes are present in *M. subandina;* according to Schiffner, who studied Raddi's specimen in the Lindenberg herbarium, the normal number of lobes in *M. papillata* is six, a larger number being unusual; according to Stephani both *M. papillata* and *M. subandina* have nine lobes apiece. In the writer's opinion nine may be regarded as the normal number of lobes, although a smaller number frequently occurs. In the number of lobes, therefore, the species agrees on the whole with *M. domingensis.* The receptacle, however, is smaller; the lobes are more dilated and more frequently emarginate at the apex; the medium protuberance of the disc and the convexity of the lobes are more pronounced; and the involucre is less variable, being entire or nearly so and apparently never bearing elongated teeth or cilia. Just how constant these differences are can only be established by the study of more material. If they should be found to intergrade it might become necessary to reduce *M. domingensis* to synonymy under *M. papillata,* but the differences seem sufficient at the present time to justify the maintenance of both species as valid.

The group of species to which *M. domingensis* and *M. papillata* belong is well represented in paleotropic regions. Among the species which are referable to this group *M. emarginata* R. Bl. & N.,[34] *M. linearis* Lehm. & Lindenb.,[35] and *M. Schaden-*

[34] Nova Acta Acad. Caes.-Leop. Carol. 12: 192. 1824.
[35] Lehmann, Pug. Plant. 4: 8. 1832.

bergii Steph.[36] may be especially mentioned. The first of these has a very extensive distribution and is reported by Stephani from China, the Himalayas, Japan, Java and the Philippine Islands; the second is known from various parts of India; the third, from the Philippine Islands only. These three species are closely related, and the differences brought out by Stephani are not very convincing. As indicated in the synonymy the authors of the Synopsis referred specimens of *M. domingensis* to *M. linearis,* an error first pointed out by Stephani. Since, however, *M. linearis* is so closely related to *M. emarginata* it will be sufficient to compare the two American plants with this latter species, a full description of which has been published by Schiffner.[37]

In size *M. emarginata* is comparable with *M. domingensis;* in the structure of the female receptacle, with *M. papillata.* It agrees with both species in the possession of sclerotic cells in the thallus; in the general features of the ventral scales; in the closely toothed appendages of the median scales; and in the structure of the involucre. Schiffner describes the latter as lobed and almost entire, but it is sometimes possible to detect a few short teeth, especially toward the outer extremities. A few differences in the structure of the thallus may be mentioned. In *M. emarginata,* for example, although sclerotic cells are present they are never so abundant or so conspicuous as they sometimes are in *M. domingensis.* The thallus is further distinguished by the possession of slime cells and, according to Schiffner, by the occasional presence of epidermal papillae. It would be unwise, however, to lay much stress on any of these differences, since the structures on which they are based are so very variable.

The female receptacle of *M. emarginata* shows the features described under *M. papillata* in an intensified form. The median protuberance is not only more pronounced, but the lobes themselves might almost be described as costate, while their apices are more markedly dilated and emarginate. These features are of course subject to variation. The male receptacles are distinguished by their long and slender stalks. The cupules are much the same as in two American species.

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[36] Bull. Herb. Boissier 7: 524. 1899.

[37] Fl. de Buitenzorg 4: 31. 1900.

8. Marchantia Bescherellei Steph.

Marchantia Bescherellei Steph. Rev. Bryol. 15: 86. 1888.

Thallus dull green, not glaucous, slightly or not at all pigmented with purple, mostly 5-7 mm. wide and 2-3 cm. long, dichotomous, the forks 1-1.5 cm. apart, texture very delicate, margin entire, sometimes vaguely and irregularly plicate; epidermis composed of cells with very thin walls, in a single layer, mostly 40-70μ long (averaging about 50μ) and 20-35μ wide (averaging about 25μ), papillae absent; pores (with their surrounding cells) mostly 160-200μ long and 120-160μ wide, surrounded usually by seven or eight rows of cells, three or four in the upper series and four in the lower series, the two lower rows of the upper series usually composed of ten to twelve or even more cells apiece, the other rows of five or six cells, rarely of only four cells apiece, inner opening usually five- or six-sided, rarely only four-sided, with the sides strongly concave, resinous deposit slight; air-chambers low, somewhat elongated, their boundaries indistinct when viewed through the epidermis, present everywhere except close to the margin, rows of photosynthetic cells usually two or three cells long; compact ventral tissue mostly twelve to fifteen cells thick in the median portion, abruptly thinning out in the wings, the walls somewhat pigmented, slightly or not at all thickened, sclerotic cells scattered, sparingly developed, slime cells lacking; ventral scales in two rows, the laminar scales alternating with the median scales and not much nearer the margin; appendages of the median scales ovate, when well developed mostly 0.5-0.6 mm. long and 0.35-0.45 mm. wide but often smaller, apex acute, margin sparingly and irregularly dentate, the teeth in the basal portion often larger and sharper and sometimes lobe-like, cells showing a gradual and slight decrease in size toward the margin, median cells usually longer than broad, mostly 50-80μ long and 30-40μ wide, marginal cells mostly 30-50μ long and 15-25μ wide, irregular but usually perpendicular or nearly so to the margin, cells containing oil-bodies lacking: male receptacle borne on a stalk about 1 cm. long (in the only example studied), with two rhizoid-furrows and (apparently) with a single broad dorsal band of air-chambers, the disc 7 mm. broad, with four short and rounded lobes or rays with thin margins, basal sinus more than 180 degrees, the other sinuses narrow, ventral scales apparently in two rows: female receptacle borne on a stalk about 2 cm. long (in the only example studied), with two rhizoid-furrows and dorsal air-chambers apparently in two distinct bands, the disc about 7 mm. wide, with five short and rounded lobes or rays, upper surface of receptacle plane, basal sinus a straight line or nearly so; involucre delicate, closely and irregularly dentate, some of the teeth three or four cells long and two to four cells wide at the base, other

teeth smaller: spores (according to Stephani) yellowish brown, 23μ in diameter, erose along the ridges, otherwise smooth. (Fig. 14.)

Known only from the following specimens:

Brazil: Rio Janeiro, *A. Glaziou 6348* (B., N. Y., type); *E. Ule 123* (B., listed by Stephani in Bull. Herb. Boissier 7: 406. 1899).

The material of *M. Bescherellei* in the Boissier herbarium, portions of which have been examined by the writer, includes the female type specimens and the male specimens collected by Ule. A sterile specimen of the type material, in the Mitten herbarium, has likewise been examined. It will be noted that Spruce,[88] who published a list of Glaziou's specimens, makes no mention of No. 6348. According to the label on the specimen in the Mitten herbarium, Spruce thought that this number might perhaps represent a new genus of the Marchantiaceae, but he evidently reached no definite conclusion about it. Probably he had only sterile material at his disposal, because the female receptacle shows at once that Stephani was correct in referring the plant to the genus *Marchantia.* Unfortunately the specimens studied by the writer were very fragmentary and remained shriveled after long soaking in water. It was therefore impossible to gain from them an adequate idea of the species, and some of the statements made about the structure must be regarded as more or less tentative.

The texture of *M. Bescherellei* is exceedingly delicate and the thallus thins out abruptly in passing from the midrib to the wings. In the latter the ventral tissue becomes reduced, according to Stephani, to a single cell in thickness, and the marginal portion, where the entire thallus is only one cell thick, is four cells broad. Although the air-chambers are low the photosynthetic tissue is well developed and characteristic and the pores are large and complex.

The appendages of the ventral scales are composed of cells which show a gradual decrease in size in passing from the median portion toward the margin, resembling in this respect the appendages of *M. domingensis* and *M. papillata,* but the margin itself is

[88] Rev. Bryol 15: 33, 34. 1888.

very different in being much more sparingly toothed. Among the preceding species the appendages find their closest counterparts in *M. paleacea* and *M. breviloba.* Their apices, however, are more uniformly sharp-pointed, their teeth tend to be sharper, and their marginal cells are more frequently placed at right angles to the margin.

With regard to the female receptacle there are marked discrepancies between Stephani's original description and the later description of his Species Hepaticarum. According to the orig-

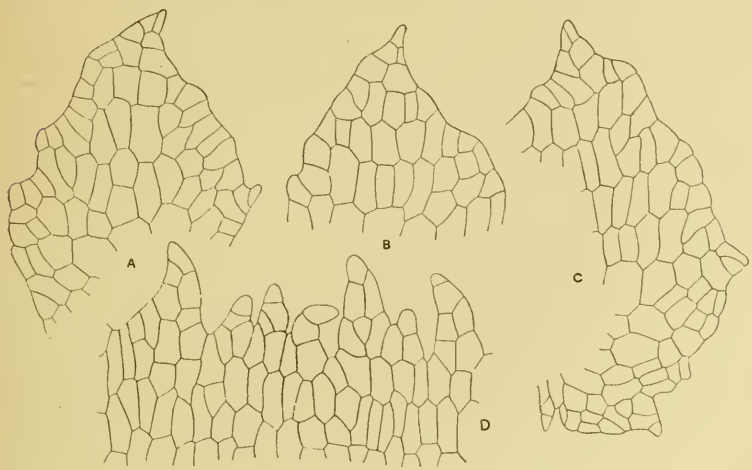

FIG. 14. MARCHANTIA BESCHERELLEI Steph.

Anatomical details. A-C. Appendages of ventral scales, x 100. D. Part of an involucre, x 100. Drawn from the type specimen.

inal account the disc is green, convex in the middle, five-lobed for one third the distance from margin to center, the lobes being rounded and shortly incised at the apex, plane and horizontal, delicate and beautifully reticulated. Doubt is thrown, however, upon the constancy of the five-lobed condition. The involucres are described as reddish, firm in texture, and shortly ciliate. According to the later account the disc is brownish green, delicate and veiny, plano-convex in the center, and nine-lobed, the lobes being plane, connate almost to the apex, rounded and very shortly incised. The involucre is said to be hyaline, small-lobed, irregularly and shortly fimbriate. In the only receptacle seen by the writer the disc is five-lobed, the two basal lobes being only about

half as broad as the other three lobes and the sinus being practically a straight line. The three broad lobes appear to be very shortly incised at the apex but they are actually only emarginate, the apparent incision being really filled by an extension of the membranous margin of the lobes. In other respects the lobes agree with Stephani's accounts. The involucre is distinctly toothed, but the teeth are scarcely long enough or sharp enough to be described as cilia or fimbriations. The discrepancy in the number of lobes which Stephani's accounts bring out might of course be due to a variability of the species, which could only become evident through the study of more extensive material.

It is unfortunate that the structure of the stalks of the receptacles must be left in doubt. In Stephani's original description the stalk of the female receptacle is said to bear two dilated dorsal lamellae but no mention is made of these in his later account, and nothing whatever is said about the structure of the stalk of the male receptacle. From the scanty supply of material available, it has been impracticable to prepare cross-sections of stalks, so that the writer is unable to confirm Stephani's statement or to add further details. If the stalk of the male receptacle bears a band of air-chambers the relationship might be with *M. domingensis.* If two bands of air-chambers are present in the stalk of the female receptacle, a relationship with *M. chenopoda* would be indicated, and it is worthy of note that Mitten referred Glaziou's type specimen to *M. brasiliensis* Lehm. & Lindenb., a species which is now included among the synonyms of *M. chenopoda* L. According to our present knowledge, however, the systematic position of the species can hardly be determined.

9. Marchantia chenopoda L.

Marchantia chenopoda L. Sp. Plant. 1137. 1753.
Marchantia androgyna L. *l. c.* 1138. 1753 (in part); Swartz, Fl. Ind. Occ. 1882. 1806.
Chlamidium indicum Corda; Opiz, Beitr. zur Naturg. 647. 1828 (*nomen nudum*).
Marchantia Swartzii Lehm. & Lindenb.; Lehmann, Pug. Plant. 4:9. 1832.
Marchantia cartilaginea Lehm. & Lindenb. *l. c.* 4:31. 1832.
Marchantia brasiliensis Lehm. & Lindenb. *l. c.* 4:32. 1832.

Grimaldia peruviana Nees & Mont.; Montagne, Fl. Boliv. in D'Orbigny, Voy. dans l'Amér. Mérid. 7²: 53. 1839.
Marchantia peruviana Nees; G. L. & N. Syn. Hep. 538. 1847.
Marchantia Dillenii Lindb. Krit. Gransk. Hist. Musc. 47. 1883.

Thallus pale or yellowish green, sometimes more or less glaucous, usually tinged with purple or brownish on the lower surface, usually 4-7 mm. wide and 2-3 cm. long, dichotomous, the successive forks averaging about 1 cm. apart, texture varying from firm and often leathery to delicate, margin entire; epidermis composed of cells with slightly thickened walls, often in two layers, mostly 30-60μ long (averaging about 40μ) and 15-30μ wide (averaging about 22μ), papillae absent, slime cells often present, averaging about 60μ in diameter; pores variable in size, usually (with their surrounding cells) measuring 100-170μ in length and 80-130μ in width but sometimes considerably smaller, usually surrounded by seven rows of cells (four in the upper series and three in the lower), more rarely by six, eight or even nine rows, the two upper rows of the upper series and the two lower rows of the lower series composed of four to six cells apiece, the third row of each series usually of twice as many, and the fourth row of the upper series usually of a much larger number, sometimes of as many as eighteen, inner opening four- to six-sided with the sides straight or more or less concave, cell-walls mostly smooth throughout; air-chambers of medium height, isodiametric or somewhat elongated, their boundaries usually distinct but sometimes obscure when viewed through the epidermis, present everywhere, cells of partition walls sometimes including slime cells, rows of photosynthetic cells usually three or four cells long; compact ventral tissue mostly twenty to twenty-five cells thick in the median portion, the walls sometimes pigmented, more or less thickened and showing distinct pits, sclerotic cells usually distinct, scattered, mostly twenty to fifty in a cross-section, usually abundant in both median portion and wings, slime cells usually present, scattered, tending to be more abundant in the wings, rarely more than six or eight in a cross-section; ventral scales in two distinct rows, the laminar scales alternating with the median scales and not much nearer the margin; appendages of the median scales very variable, lanceolate to broadly ovate, when well developed mostly 0.45-0.65 mm. long and 0.3-0.4 mm. wide but sometimes considerably smaller, apex acuminate, acute or apiculate, margin entire or variously and irregularly toothed, the teeth rarely numerous and often restricted to the basal portion, cells of about the same size throughout or showing a slight and gradual decrease in size toward the margin, median cells usually longer than broad, mostly 60-90μ long and 25-40μ wide, marginal cells mostly 30-70μ

long and 20-35μ wide, irregular, the long axis varying from parallel to perpendicular to the margin, cells containing oil-bodies usually absent, rarely one or two present: male receptacle borne on a stalk mostly 1-2 cm. long, with two rhizoid-furrows and no air-chambers, the disc mostly 0.8-1 cm. broad, deeply lobed, the lobes or rays mostly four, rarely five or six, palmately disposed, the basal sinus sometimes more than 180 degrees broad, the lobes mostly 5-7 mm. long and 1.5-2 mm. wide, rounded, with a thin wavy margin extending across the basal sinus, ventral scales imbricated, mostly in two rows: female receptacle borne on a stalk 2-4 cm. high, with two rhizoid-furrows and two narrow dorsal bands of air-chambers, the disc convex, mostly 6-8 mm. wide, shortly five-lobed, the lobes or rays convex, rounded and separated by shallow sinuses, the basal sinus much broader than the others and approximating a straight line; involucre firm, the margin sparingly dentate to closely ciliate or laciniate, the teeth or cilia varying from one to five cells in length, sometimes forking; spores brownish yellow, about 26μ in diameter, narrowly margined, the outer face bearing a few low ridges not forming a network; elaters about 6μ wide, bispiral: cupules closely short-ciliate, the cilia mostly two to four cells long, outer surface without papillae. (Figs. 15-20.)

A widely distributed species is tropical America. The following specimens have been examined:

Puebla: banks of Avenida Hidalgo and path to barranca, Tezuitlan, October, 1908, *Barnes & Land 537.*

Vera Cruz: Jalapa and vicinity, September, 1906, *Barnes & Land,* no number (Y.); July, 1908, *C. G. Pringle 15326* (Y., distributed in Pl. Mex. under a manuscript name of Stephani); November, 1908, *Barnes & Land 556, 614, 626a* (Y.); vicinity of Orizaba, November, 1908, *Barnes & Land 631, 670* (Y.).

Guatemala: without definite locality or date, *Godman & Sabin* (N. Y.); Santa Rosa, September, 1894, *Heyde & Lux 6293* (N. Y.); near the Finca Sepacuité, Alta Verapaz, March and April, 1902, *Cook & Griggs 83, 141, 394* (U. S., Y.); trail from Pangós to Sepacuité, Alta Verapaz, January, 1908, *Maxon & Hay 3111* (U. S., Y.); Coban, Alta Verapaz, *H. von Tuerckheim 6074* (N. Y.).

Costa Rica: Bagnar, Angostura, June, 1874, *O. Kuntze 2102* (N. Y.); la Verbena, Alajuelita, August, 1894, *A. Tonduz 15562* (N. Y., Y., distributed by E. Levier under a manuscript name of Stephani); Rio Turrialba, March, 1896, *J. D. Smith* (N. Y.); Cuesta de la Vieja, road to San Carbos, April, 1903,

Cook & Doyle 111 (U. S., Y.); Juan Vinas, April, 1903, *Cook & Doyle 301* (U. S., Y.); vicinity of La Palma, May, 1906, *W. R. Maxon 489* (U. S., Y.).

PANAMA: without definite locality or date, *B. Seemann* (N. Y.); Darien, April and June, 1908, *R. S. Williams 1083, 1084* (N. Y., Y.).

CUBA: without definite localities or dates, *C. Wright* (distributed in Hep. Cubenses).

JAMAICA: without definite localities or dates, *Fordyce, W. Wright;* Whitfield Hall, December, 1896, *W. Harris 11063* in part (N. Y.); Moody's Gap, March, 1895, *W. Harris 5671* (N. Y., U. S., Y.); vicinity of Cinchona, November, 1902, *F. S. Earle 397a* (N. Y., Y.); July, 1903, *A. W. Evans 248* (Y.); Mount Airy, trail to Tweedside, April, 1903, *W. R. Maxon 864* (U. S., Y.); Second Breakfast Spring, near Tweedside, April, 1903, *W. R. Maxon 880* (U. S., Y.); Morce's Gap, August, 1906, *A. W. Evans 405* (Y.); Cuna Cuna Gap, September, 1908, *E. G. Britton 990* (N. Y., Y.); March, 1909, *Britton & Howe 4032* (N. Y., Y.).

PORTO RICO: Adjuntas, March, 1886, *P. Sintenis 51* (N. Y., U. S., Y., listed by Stephani in Hedwigia 27: 294. 1888); road from Ponce to Adjuntas, July, 1901, *Underwood & Griggs 732* (N. Y., U. S., Y.); Military Road, north of Cayey, June, 1901, *Underwood & Griggs 278* (U. S., Y.); road from Utuado to Arecibo, July, 1901, *Underwood & Griggs 839* (U. S., Y.); near Cayey, July, 1900, *A. W. Evans 95* (Y.); between Ponce and Utuado, March, 1906, *Britton & Marble 778* (N. Y., Y.); Mount Morales, near Utuado, March, 1906, *M. A. Howe 1098* (C. C. H., N. Y., Y.); summit of Loma la Mina, Sierra de Naguabo, July, 1914, *J. A. Shafer 3337* (N. Y., Y.); La Juanita, near Las Marias, February, 1915, *E. G. Britton 3964* (N. Y., Y.); La Chiquita, near Maricao, February, 1915, *E. G. Britton 4099* (N. Y., Y.); *Britton & Cowell 4296* (N. Y., Y.); between Adjuntas and Ponce, March, 1915, *E. G. Britton 5367* (N. Y., Y.): Maricao, July, 1915, *F. L. Stevens 1844* (N. Y., Y.); Gigante, July, 1915, *F. L. Stevens 1797* (N. Y., Y.).

GUADELOUPE: without definite locality, 1874, *T. Husnot* (distributed in Pl. des Antilles *196*); Gombeyre, 1897-1900, *Père Duss 391* (N. Y.); Basse Terre, 1898 *Père Duss 253* (N. Y., determined as *M. brasiliensis* by Stephani).

Dominica: Laudat, 1903, *F. E. Lloyd 76, 78, 285* (N. Y., Y.). Martinique: St. Pierre, 1899-1900, *Père Duss 390* (N. Y.,

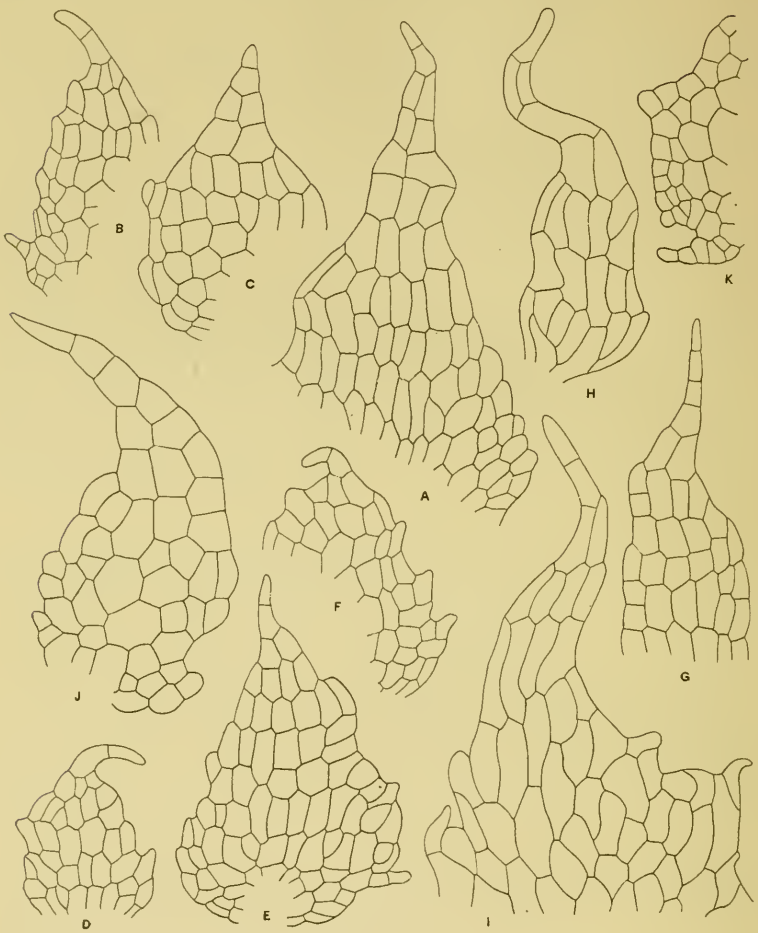

Fig. 15. Marchantia chenopoda L.

Appendages of ventral scales, x 100; K represents the basal portion of an appendage. A. Vera Cruz, 1906, *Barnes & Land.* B-G. Vera Cruz, *Barnes & Land 614.* H, I. Vera Cruz, *Barnes & Land 626a.* J, K. Guatemala, *Cook & Griggs 83.*

determined as *M. brasiliensis* by Stephani); Carbet, 1899, *Père Duss 342 bis* (N. Y.); Morne Rouge, August, 1901, *Père Duss 581* (N. Y.).

GRENADA: Grand Etang, 1913, *R. Thaxter* (H., Y.).

VENEZUELA: near Caripe, *A. von Humboldt* (Y., specimen from the Hooker herbarium, labeled *"Humboldt 235,"* presumably the basis for the record in Nov. Gen. Sp. Plant. 7:99. 1825); without definite locality or date, *Funck & Schlim 337* (N. Y.).

COLOMBIA: Andes Bogotenses, *W. Weir* (N. Y.).

BRAZIL: Orgaos Mountains, *C. Gaudichaud* (N. Y., specimen from the Montagne herbarium, labeled simply *"Brasilia,"* presumably the basis for the record in Voy. Corv. la Bonité, Bot. 1:209. 1844-46); Morro Velho, no date, *G. Gardner 131* (N. Y.); Rio de Janeiro, no date, *J. Milne* (N. Y.); *A. Glaziou 17992* (N. Y., listed by Spruce in Rev. Bryol. 20:60. 1893); Jacobina, Mattogrosso, October, 1872, *O. Kuntze* (N. Y., sterile and somewhat doubtful); near Sao Paulo, April, 1905, *A. Usteri 1* (Y.).

ECUADOR: Baños, *R. Spruce* (listed in Trans. Bot. Soc. Edinburgh 15:562. 1885, and distributed in Hep. Spruceanae).

PERU: near Tarapoto, *R. Spruce* (distributed in Hep. Spruceanae); Ollantaytambo, May, 1915, *Cook & Gilbert 755* (U. S., Y.).

BOLIVIA: near Irupana, *A. d'Orbigny 226* (M., type of *Grimaldia peruviana*); Yungas, 1885, *H. H. Rusby, 3001, 3002, 3003, 3004* (N. Y., U. S., listed by Spruce in Mem. Torrey Club 1:140. 1890); 1892, *M. Bang 1545* (N. Y.); July, 1893, *P. Jay 71* (N. Y., Y.); Tumupasa, December, 1901, *R. S. Williams 2143* (N. Y., Y.).

GALAPAGOS ISLANDS: Albemarle Island, August, 1906, *A. Stewart 6876.*

The following additional stations, recorded in the literature, are likewise of interest:

OAXACA: Mirador and Comaltepec, *F. Liebmann* (listed by Gottsche in Mex. Leverm. 268. 1863).

VERA CRUZ: near Orizaba and at Cordoba, 1855, *F. Müller* (listed by Gottsche, *l. c.*).

COSTA RICA: near San José, *H. Pittier 6004, 6049;* Marais de la Palma, *H. Pittier 6018, 6024* (both listed by Stephani in Bull. Soc. Bot. Belgique 31:180. 1892).

JAMAICA: without definite locality or date, *P. Collinson* (type of *M. Dillenii*).

MARTINIQUE: Morne de la Calabasse, without date or collector's name (type, cited by Plumier); without definite locality, date, or collector's name (type of *M. cartilaginea*); without definite locality or date, *Hahn 1347; T. Husnot 197, 198* (the last three listed by Bescherelle in Jour. de Bot. 7: 193. 1893).

FRENCH GUIANA: near Cayenne, 1835-49, *Leprieur 1386* (listed by Montagne in Ann. Sci. Nat. Bot. IV. 3: 320. 1855).

VENEZUELA: Merida, *K. Goebel* (figured in Organographie der Pflanzen 258. *f. 157.* 1898).

COLOMBIA: Muzo, Fusagasuga and Puripi, 1859, *A. Lindig 1715, 1718, 1719, 1722, 1723* (listed by Gottsche in Ann. Sci. Nat. Bot. V. 1: 186. 1864).

PERU: Rio Huallaga, November, 1902, *E. Ule 527* (listed by Stephani in Hedwigia 44: 223. 1905).

BRAZIL: "Montagne d'Estrella," *G. Raddi* (cited by Raddi, see below); without definite locality or date, *F. Sellow* (type of *M. brasiliensis*).

The specimens recorded by Schiffner from the Fiji Islands (Leberm. Forschungsr. S. M. S. "Gazelle" 43. 1890) are described as having ciliate-dentate ventral scales and would probably now be referred to some other species.

The interpretation of *M. chenopoda* is beset with difficulties, and a history of the species may therefore be in place. The Linnaean description or diagnosis is very short and reads, "Marchantia calyce communi dimidiato palmato quadrifido." If the term "calyx" signifies the female receptacle this description would not apply accurately to any of the known American species, where a four-parted receptacle occurs only as an abnormality. If the term signifies the male receptacle there are several species to which the description might perhaps apply. In any case it would be quite impossible to identify a definite species by means of the Linnaean description alone.

Unfortunately the only synonym which Linnaeus quotes, the "Lichen anapodocarpos" of Plumier, is likewise insufficient to lead to a positive conclusion. Plumier[39] described his plant from material collected on the Morne de la Calabasse in Martinique. Linnaeus cites the original description and figure and also the

[39] Traité des Fougères de l'Amér. 143. *pl. 142.* Paris, 1705.

later description and figure published by Dillenius.[40] Plumier's figure represents certain reproductive parts in detail and a thallus with a sinuate or vaguely lobed margin, branching occasionally by forking and apparently also by ventral outgrowths. From the tips of some of the branches the four-lobed receptacles on short stalks take their origin and clearly bring the growth of the branches to an end. In two cases—possibly in three—five-lobed receptacles are shown. In his text Plumier compares the appearance of the plant with that of the Indian fig and says that the upper surface is of a pale green color and roughened by minute elevated points. He compares the entire receptacle with a mushroom and states that one side of the disc is rounded, while the other shows four semicircular lobes, the whole resembling an inverted goose foot. He adds that each lobe opens longitudinally, and shows minute white "flowers" in the form of tubes. Each tube divides at the apex after a while into four parts which roll back and disclose an oval fruit filled with "seeds" like flour. It is clear from this account that he had female receptacles before him and that he saw the involucre, the pseudoperianth, the capsule, and the spores.

Dillenius took his figure directly from Plumier and did not know the plant itself. He tried to improve the figure, however, by indicating that the upper surface of the thallus was covered over with minute polygons as in related species. Lindberg[41] criticises the figure of Dillenius (and consequently that of Plumier) by stating that an autoicous inflorescence is shown, both male and female receptacles being represented on the thallus. This criticism is undeserved. The receptacles shown are all female, the dorsal surface being represented in some cases and the ventral in others. In his text Dillenius brought out the fact that the receptacles were all the same kind, although he incorrectly interpreted the fruit of Plumier as an anther and the flour-like seeds as pollen, a well-known error which he repeats in his interpretation of the reproductive parts in other bryophytes.

On the basis of Plumier's description and figures it becomes evident that the term "calyx" in the Linnaean diagnosis of *M.*

[40] Hist. Musc. 531. *pl. 75, f. 5.* Oxford, 1741.
[41] Krit. Gransk. Dillen. Hist. Musc. 45. Helsingfors, 1883.

chenopoda refers to the female receptacle, and it has already been pointed out that a quadrifid female receptacle is not found

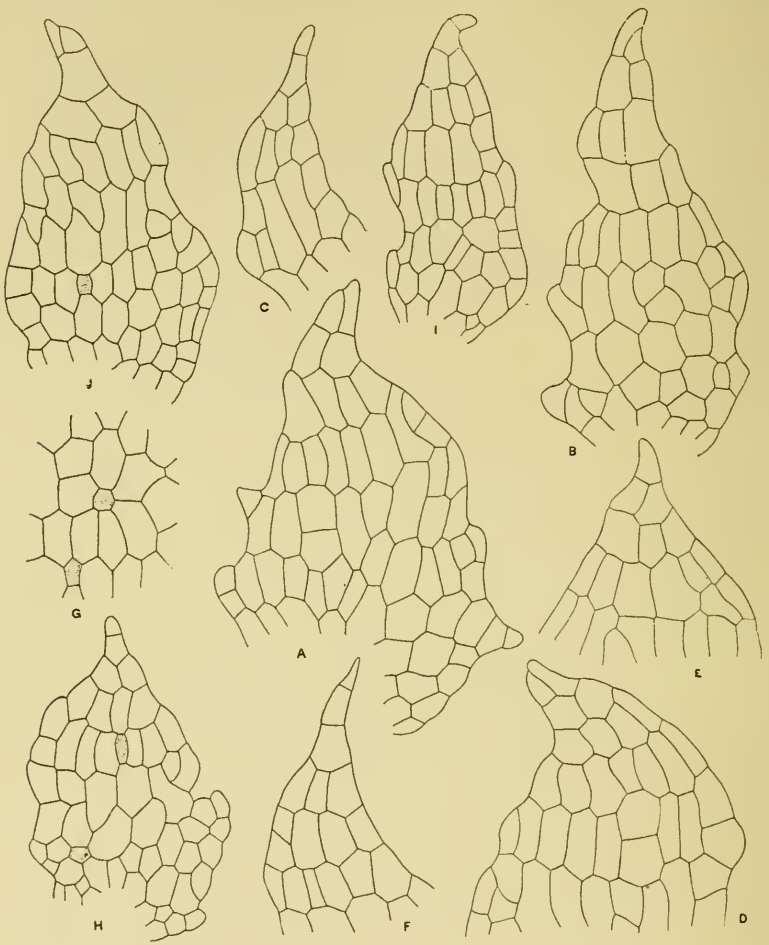

FIG. 16. MARCHANTIA CHENOPODA L.

Appendages of ventral scales, x 100; G represents the median portion of an appendage with two cells containing oil-bodies. A-C. Cuba, *C. Wright,* in Hep. Cubenses. D, E. Jamaica, *A. W. Evans 258.* F, G. Jamaica, *W. R. Maxon 405.* H, I. Porto Rico, *F. L. Stevens 1844;* J. Guadeloupe, *T. Husnot,* in Pl. des Antilles *196.*

normally in any known American species. Plumier's work indicates further, that the involucres and sporophytes of his plant are situated underneath the lobes, a condition which is likewise

unknown among American species, where the involucres and sporophytes invariably alternate with the lobes. Since there are apparently no specimens of Plumier's plant in herbaria, it is clear that *M. chenopoda* L. represents an unidentifiable plant, and the logical course would be to give up the species altogether.

In the literature of the Hepaticae, however, *M. chenopoda* has an established place, and it seems justifiable to interpret it according to the descriptions of later writers. Even Plumier's figure gives us a little help because it shows that he occasionally observed a five-lobed receptacle, although he makes no mention of such a structure in his text. Since most subsequent writers ascribe to the species definitely a five-lobed receptacle, and since the species to which they assign the name is abundant in Martinique, it is quite probable that their *M. chenopoda* is the same as Plumier's plant. Unfortunately their descriptions and figures are not without discrepancies, and it becomes evident that Taylor at least did not distinguish between what is here called *M. chenopoda* and *M. domingensis.*

Apparently Swartz[42] was the first to describe the male receptacles. He states that they are subpeltate, unsymmetrical, palmate-quadrifid, plane and verruculose above (like the thallus), and convex below, the rays or lobes being linear, obtuse, and often unequal, with membranous, undulate margins. He cites no stations for the species although he implies that it occurs in Jamaica. Quadrifid receptacles are sometimes found in *M. domingensis,* but it is probable that Swartz had the true *M. chenopoda* before him, and his description is definitely cited in the Synopsis Hepaticarum.

Schwaegrichen,[43] in 1814, quotes *M. chenopoda* from Africa as well as from America, and F. Weber,[44] the following year, notes a similar extension of range. Neither writer adds anything significant to our knowledge of the species, and it is probable that their citation of African stations is based on incorrect determinations, since all subsequent writers restrict the range of *M. chenopoda* to America.

A few years later Raddi[45] extended the known range of the

[42] Fl. Ind. Occid. 1880. Erlangen, 1806.
[43] Hist. Musc. Hepat. Prodr. 32. Leipzig, 1814.
[44] Hist. Musc. Hepat. Prodr. 103. Kiel, 1815.
[45] Mem. Soc. Ital. Modena 19:44. 1823; 20: *pl. 6a, f. 1, 2.* 1829.

species into Brazil and stated that it occurred abundantly at the bottom of moist and mossy rocks on the "Montagne d'Estrella." According to his account *M. chenopoda* is distinguished from all the other species of *Marchantia* by its receptacles, which are truncate on one side. He adds that in the male receptacle the upper surface is plane and that the four parts or lobes are unequal in length, and he criticises Plumier for comparing this receptacle with a goose's foot; in his opinion it is more like the foot of a pigeon. Of course this criticism has no weight, since Plumier drew his account entirely from female receptacles. According to Raddi the disc of the female receptacle is strongly convex and either entire or very shortly divided, bearing on the lower surface four fleshy or rib-like swellings, between which are borne the capsules, much as in *M. polymorpha.* He notes further that the upper surface of the thallus is areolate and perforated by white vesicles and that the lower surface is violet except along the margin, where it is green. Although Raddi's specimens have not been available for study it is evident that he had the true *M. chenopoda* before him. Not only is his description unusually clear, but the species has since been collected in other Brazilian localities.

In 1835 Taylor published an account of the Marchantiaceae which had come under his observation. In his description of *M. chenopoda*[46] he comments on the inaccuracies of Plumier's figures and quotes them doubtfully, although it was upon Plumier's work that the species was primarily based. According to Taylor the female receptacle is hemispherical and divided into from eight to ten truncate laciniae, each bearing underneath a single involucre with ciliate or serrulate margins. He notes further that the stalk of the receptacle has two rhizoid-furrows and adds interesting statements about the scales on the vegetative thallus and about the cupules. The scales, in his words, have an entire and broadly ovate base, then a deep constriction at about the middle, and then a broadly ovate and ciliate expansion (the latter being what is now known as the appendage). In the cupules he speaks particularly of the serrate margin. It will be seen at once that Taylor's account of the female receptacle is very different from that of his predecessors, and the specimens in his herbarium show that it was drawn from *M. domin-*

[46] Trans. Linn. Soc. 17:379. *pl. 12, f. 2.* 1835.

gensis. His account of the male receptacle, however, agrees esentially with that of Swartz. Taylor cites *M. chenopoda* from

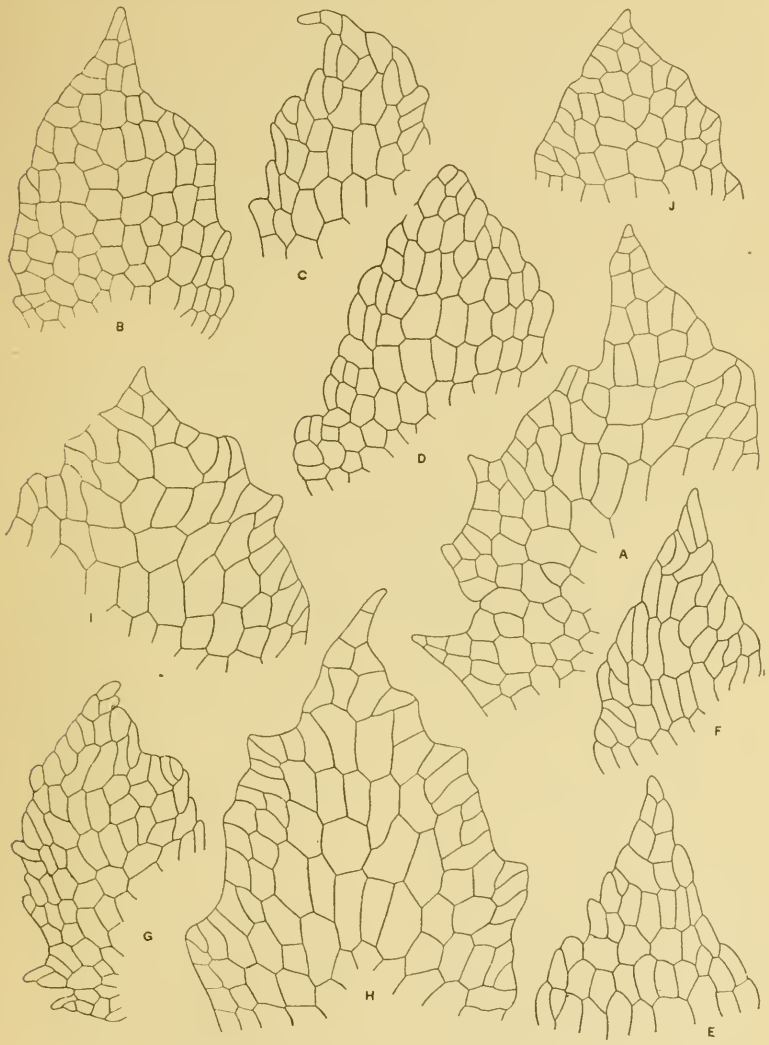

FIG. 17. MARCHANTIA CHENOPODA L.

Appendages of ventral scales, x 100. A, B. Venezuela, *Funck & Schlim.* C-E. Brazil, *A. Glaziou 17992.* F, G. Brazil, 1905, *A. Usteri 1.* H-J. Galapagos Islands, *A. Stewart 6876.*

Guadeloupe and St. Vincent as well as from Jamaica and Martinique.

In the Synopsis Hepaticarum emphasis is again laid on the receptacles. The female receptacle is said to be excentric, hemispherical, and about five-lobed, the lobes being obtuse, subcrenate and soon obsolete, with hyaline, denticulate involucres. The male receptacles are said to be unsymmetrical and palmately four- to five-parted. This account of the female receptacle agrees closely with that of Raddi and differs from that of Taylor. Both writers, however, are cited under the species. From Brazil several localities are enumerated, but the only West Indian stations given without question are on the island of Martinique. The Synopsis quotes three synonyms: *M. androgyna* (female plants only), *M. Swartzii,* and *Chlamidium indicum.* These may be considered in order.

Swartz apparently supposed that what he called *M. androgyna* was the same as *M. androgyna* L.,[47] a species based on two citations, the first from Dillenius[48] and the second from Micheli.[49] According to Swartz, who treats the plant very briefly, *M. androgyna* is related to *Reboulia hemisphaerica* (L.) Raddi; he describes the thallus as narrower than in that species and states that the male receptacles are perhaps sessile and that the female receptacles are subentire. Although he cites no actual material it is probable that he drew his description from Jamaican specimens collected by himself, these being definitely referred to by later writers.

Now the Dillenian species quoted by Linnaeus under *M. androgyna* has been the cause of a great deal of confusion. It was based on two entirely different plants, a fact which was first pointed out by Lehmann and Lindenberg in their discussion of the Asiatic *M. linearis* Lehm. & Lindenb.[50] They show clearly that the Dillenian *f. 3B,* which, as they state, is essentially the same as the figure by Micheli, represents *Grimaldia dichotoma* Raddi, a common species of the Mediterranean region. They show further that the Dillenian *f. 3A* and *f. 3C* represent a species of *Marchantia,* and they suppose that this species is the same as the *M. androgyna* of Swartz. The two figures in question were drawn from specimens collected in Jamaica by P. Collinson;

[47] Sp. Plant. 1138. 1753.
[48] Hist. Musc. 520. *pl. 75, f. 3.* 1741.
[49] Gen. Nov. Plant. 3. *pl. 2, f. 3.* 1729.
[50] Lehmann, Pug. Plant. 4:9. Hamburg, 1832.

f. 3A shows a plant with numerous cupules and female receptacles, while *f. 3C* shows a small forking fragment with cupules

FIG. 18. MARCHANTIA CHENOPODA L.

Appendages of ventral scales, x 100. A-C. Peru, *Cook & Gilbert 755*. D-F. Bolivia, *A. d'Orbigny*, type of *M. peruviana*. G, H. Bolivia, *H. H. Rusby 3004*. I, J. Bolivia, *P. Jay 71*.

only. The receptacles are so strongly convex that they appear conical and resemble those of *Conocephalum conicum* (L.) Dumort. In fact, according to Lehmann and Lindenberg, the

M. androgyna of Weber[51] is actually *Conocephalum conicum,* and the Linnaean name has been applied by other writers to such distinct species as *Preissia quadrata* (Scop.) Corda and *Reboulia hemisphaerica* (L.) Raddi.

Lehmann and Lindenberg's conception of *M. androgyna* Sw. was based on specimens collected by Swartz in Jamaica. Although they considered these specimens identical with those collected by Collinson they did not take up the name *M. androgyna* for the species, probably because the original *M. androgyna* L. was an aggregate. They described it instead under the new name *M. Swartzii.* The female receptacle, according to their account, is unsymmetrical, hemispherical, and subentire or obsoletely lobed, the lower surface and the stalk being villous. They state further that the upper surface of the thallus is green with many large pores bordered with white, and that the lower surface is brown with scales in the median portion; and they suggest that the male receptacles of Swartz's description may have been cupules only. So far as the descriptions go *M. Swartzii* and, consequently, *M. androgyna* Sw. do not differ in any essential respects from *M. chenopoda,* and the authors of the Synopsis are probably correct in citing these two species as synonyms of *M. chenopoda.* This view is supported by a fragmentary specimen in the Taylor herbarium, labeled *M. Swartzii* by Lehmann, which apparently represents *M. chenopoda,* although a positive conclusion can hardly be reached without sectioning the material.

A further difficulty in disentangling the synonymy is, however, encountered. Although Lehmann and Lindenberg considered Swartz's and Collinson's plants identical, this opinion was not shared by the authors of the Synopsis Hepaticarum. In quoting *M. Swartzii* as a synonym of *M. chenopoda* they take pains to exclude the Dillenian *f. 3* altogether, although *f. 3A* and *f. 3C* are definitely quoted by the authors of *M. Swartzii* in citing *M. androgyna* Sw. as a synonym of their species. Fortunately Collinson's material is preserved in the Dillenian herbarium and throws a little light on the subject. It was studied by Lindberg, who reached the conclusion that it represented a distinct and undescribed species. This he proposed as new under the name *M. Dillenii* Lindb. He assigns to

[51] Spic. Fl. Goettingen. 168. Gotha, 1778.

the species a delicate pellucid thallus with indistinct areolae but with large pores, the thallus in *M. chenopoda* being thick and

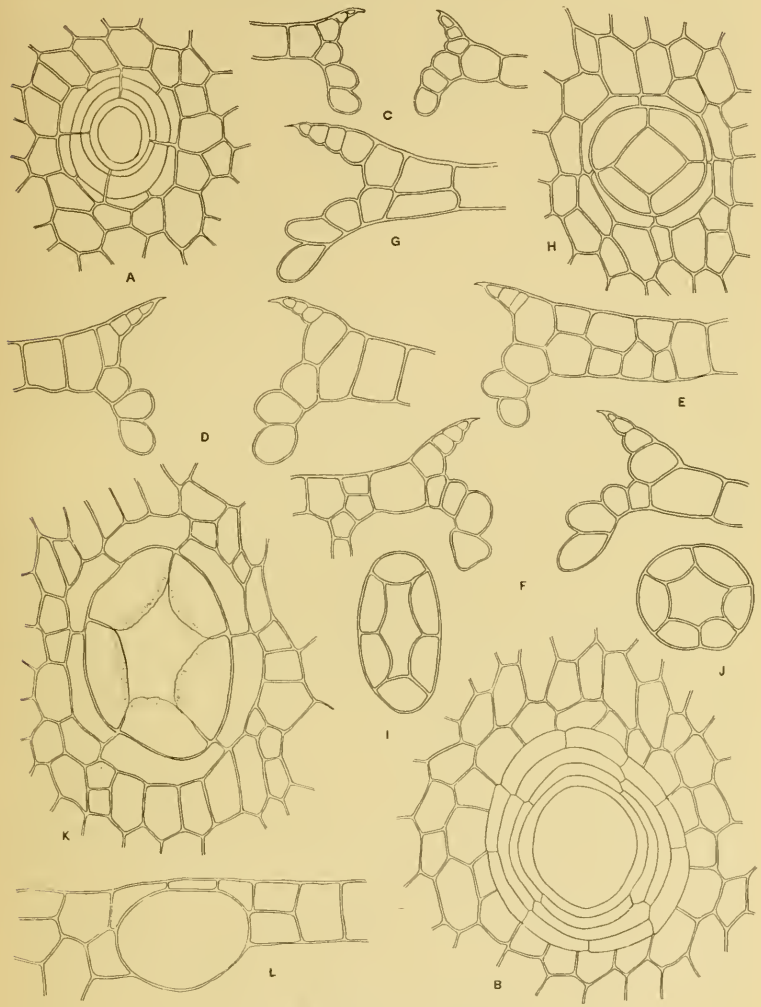

FIG. 19. MARCHANTIA CHENOPODA L.

Epidermal structures of thallus, x 225. A, B. Pores, surface view. C-G. Pores, cross-section. H-K. Pores, inner view. L. Slime cell, cross-section. A, C, H-J. Guatemala, *Cook & Griggs 83*. B, D, E, K, L. Jamaica, *W. R. Maxon 405*. F, G. Peru, *Cook & Gilbert 755*.

opaque with distinct areolae and small pores. He states further that the female receptacles are depressed-semiglobose, excentric and almost entire, the five lobes present being very short, thick,

semicircular in outline and slightly incurved. The receptacles described are immature and do not therefore yield very satisfactory characters, but Lindberg's description, so far as it goes, would clearly apply to *M. chenopoda.* Even the characters drawn from the thallus easily come within the range of variation to be expected in so multiform a species, where both the texture and the size of the pores differ widely in different plants. The writer would therefore follow Stephani in reducing *M. Dillenii* to synonymy, even in the absence of Lindberg's type material.

The third synonym given in the Synopsis, *Chlamidium indicum,* is nothing but a *nomen nudum.* According to Corda it was based on No. 375 of Sieber's Flora Martinicensis. The Synopsis, however, in citing it as a synonym under *M. chenopoda,* states that it was based on No. 378. In the Mitten herbarium a specimen of No. 378 is preserved under the name *M. martinicensis.* This plant, which probably represents the type of the manuscript species *M. martinicensis* Spreng., is clearly referable to *M. domingensis,* as the authors of the Synopsis have already shown. Their citation of No. 378 under *Chlamidium indicum,* therefore, was probably an error or due to the fact that this number was a mixture; in any case Corda's species, in the absence of adequate publication, deserves no further attention.

If the work of Taylor is excepted it will be seen that writers up to the time of the Synopsis Hepaticarum (1847) were practically unanimous in assigning to *M. chenopoda* a subentire or shortly five-lobed female receptacle and a deeply four-cleft male receptacle. The same thing may be said of subsequent writers. Unfortunately identical or similar characters have been assigned to other species. Aside from *M. Dillenii,* which has already been alluded to, *M. cartilaginea, M. brasiliensis,* and *M. peruviana* may be mentioned in this connection. The first was based on material collected on the island of St. Vincent, no collector being named; the second on Brazilian material collected by Sellow; the third on Bolivian material collected by D'Orbigny.

In *M. cartilaginea* the male receptacles are said by the authors of the species to be slightly convex and borne on very short stalks, while the female receptacles are said to be minute and entire or obsoletely crenulate. Schiffner, who studied the type material, found that the female receptacles were immature and that the so-called male receptacles were nothing more than

extremely young female receptacles. The distinctive characters of the species thus break down, and he reduced it to synonymy, retaining it as a var. *cartilaginea* (Lehm. & Lindenb.) Schiffn. under *M. chenopoda.* Stephani quotes it as a simple synonym. Their views are supported by the work of Prescher, who found the distribution of the slime cells the same in *M. cartilaginea* as in *M. chenopoda.*

In *M. brasiliensis* the male receptacle is described as peltate, angled and convex, the central portion being thickened and the margin plane and hyaline; the female receptacle is said to be hemispherical, symmetrical and entire. Here again Schiffner showed that the receptacles in the type specimen were immature and that the distinctive characters drawn from the male receptacles could be duplicated by young male receptacles of *M. chenopoda.* He therefore regards *M. brasiliensis* as synonymous with *M. chenopoda,* a view which the writer is disposed to share. Stephani, in maintaining the validity of the Brazilian plant, dwells on the symmetry of the female receptacle and describes it as strongly convex and very shortly four- to six-lobed. He adds that the entire appendages of the ventral scales can easily be distinguished from the dentate appendages of *M. chenopoda.* Since, however, he assigns both entire and toothed appendages to *M. chenopoda* in his detailed description of that species, and since the receptacles on some of the West Indian specimens referred by him to *M. brasiliensis* are distinctly unsymmetrical, his differential characters can not be regarded as having much significance.

In the original description of *Grimaldia peruviana* the female receptacle is said to be subglobose and crenate while the male receptacle is said to be discoid and sessile. Apparently on account of the characters of the so-called male receptacles Montagne continued to regard the species as a *Grimaldia* even after the authors of the Synopsis had correctly transferred it to *Marchantia.*[52] Probably the sessile structures which Montagne observed were immature female receptacles, but unfortunately the type specimen in his herbarium, a portion of which the writer has been able to examine, is sterile, so that these problematical organs could not be studied. The compound pores, however,

[52] See Montagne, Sylloge 91. Paris, 1856.

and the cupules show conclusively that the species is a *Marchantia,* and the writer would go even further than Stephani did and reduce it to a synonym of *M. chenopoda.* This conclusion is strengthened by the fact that numerous specimens of *M. chenopoda* have been collected in Bolivia by subsequent explorers.

Although a wide range of variability is assigned to *M. chenopoda,* according to the writer's conception of the species, an equally wide range is assigned to *M. domingensis* and an even wider range to *M. polymorpha.* The structures which are perhaps most subject to variation are the epidermal pores, the slime cells, the appendages of the ventral scales and the involucres. The male receptacles and the female receptacles in most respects exhibit features of a more constant character.

In normal and well-developed specimens the pores are unusually large in the middle of the thallus and are only slightly smaller near the margin. In other cases the contrast in size between the median and marginal pores is much more marked; in still other cases even the median pores may be small or medium sized. Corresponding with these differences in size there are differences in the number of cells in the concentric rows around the opening, although the number of such rows is usually seven. The differences in number are found especially in the third and fourth rows of the upper series and in the third row of the inner series. In the fourth row of the outer series the variation is especially great. In small pores as few as four cells may be present, in large pores as many as eighteen cells, and all gradations between these extremes are to be expected. In the third row of each series similar but less marked differences are encountered. In the first and second row of each series four cells are normally present although three, five, six, or even seven cells sometimes occur.

The slime cells vary greatly in number and in distribution. In typical West Indian material they occur abundantly in the epidermis, in the walls of the air-chambers, and in the compact ventral tissue of the thallus. In other specimens they are rare in the epidermis or even absent altogether, although still persistent in the walls of the air-chamber and in the compact tissue; in still other specimens, and this seems to be especially true of material from Mexico, Central America and South America, they are restricted to the compact tissue, where indeed they may be

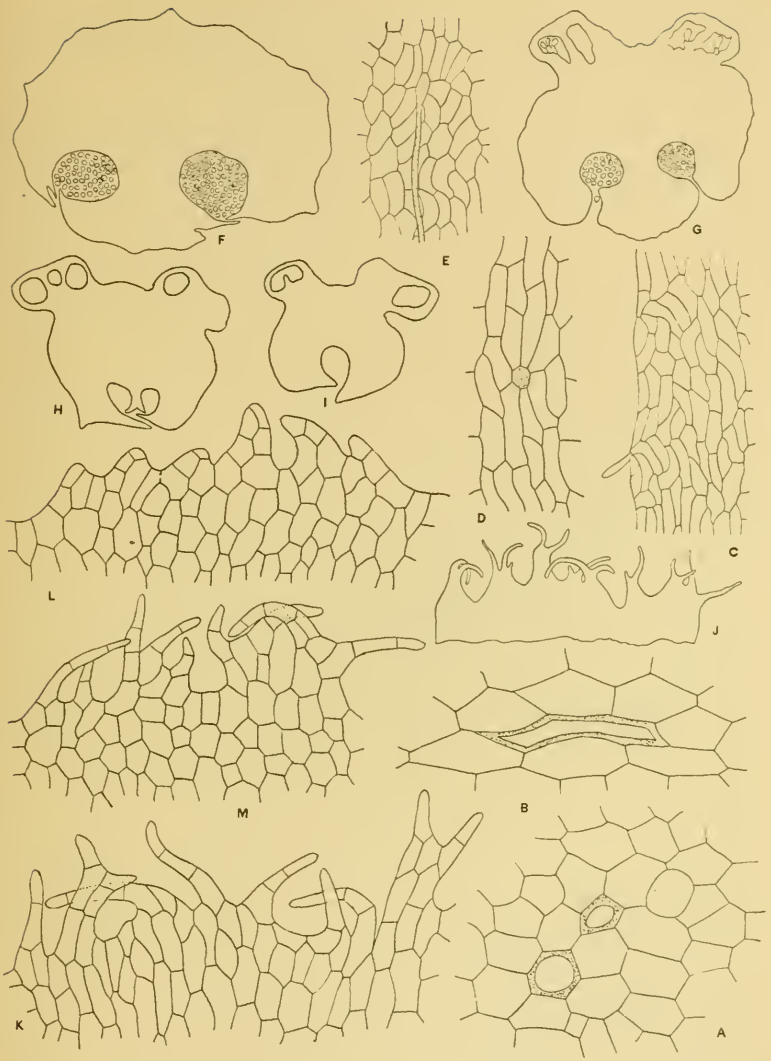

FIG. 20. MARCHANTIA CHENOPODA L.

Anatomical details. A. Cells from compact ventral tissue in cross-section, including two sclerotic cells and a cell containing oil-bodies, x 100. B. Cells from same tissue in longitudinal section, including a sclerotic cell, x 100. C-E. Cells from basal portions of median scales, x 100. F. Stalk of male receptacle, cross-section, x 50. G-I. Stalks of female receptacles, cross-sections, x 50: G, showing a stalk of average size; H, a slender stalk near the middle; and I, the same slender stalk near the base. J-M. Portions of involucres: J, x 40; L-M, x 100. A-G, J. Jamaica, *A. W. Evans 405, W. R. Maxon 880.* H, I. Panama, *R. S. Williams 1084.* K. Vera Cruz, *Barnes & Land 631.* L. Costa Rica, *Cook & Doyle 301.* M. Bolivia, *R. S. Williams 2143.*

very scarce. Since these different conditions grade into one another, it seems impossible to use them as a basis for the segregation of *M. chenopoda.*

Very striking variations are to be observed in the appendages of the median scales. If the series represented in Figs. 15-19 is examined it will hardly seem possible at first that all can have been taken from a single species. The appendages shown exhibit four more or less distinct types, varying in shape, in the character of the margin, and in the size of the component cells. In the first type, shown by Figs. 15, A-H, and 16, the appendages are narrowly ovate to lanceolate, tapering gradually to an acute or acuminate apex; the margin is either entire or provided with one or more vaguely defined and irregular teeth; and the cells are large, showing no marked differences in size between the median and marginal portions. In the second type, shown in Figs 15, I, and 17, A, the appendages are larger than in the first type and tend to be more acuminate; the margin is more distinctly dentate, although the teeth are still irregular; and the cells are much the same as in the first type, except for the fact that the marginal cells in the basal portion tend to be smaller. In the third type, shown in Fig. 18, A-C, the appendages are broadly ovate and apiculate to abruptly acute; the margin is entire or vaguely and sparingly dentate or crenate toward the base; and the cells are everywhere large, much as in the first type. In the fourth type, shown in Fig. 18, D-J, the appendages have about the same form as in the third type, although they sometimes taper more gradually; but the margin is more irregular, varying from entire to distinctly and rather closely crenate, dentate, or even lobed in the basal portion; and the cells are distinctly smaller, often showing a definite decrease in size between the median and marginal portions. Cells containing oil-bodies are usually absent altogether, but one or two sometimes occur, as shown in Fig. 16, G, H, J. These have not been observed except in the first type of appendage.

Since the various types of appendage are more or less characteristic of definite regions, the first type, for example, being prevalent in the West Indies and the fourth in South America, the writer at first thought that distinct varieties with definite geographical ranges might be distinguished, using the appendicular differences as a basis. It soon became evident, however,

that this was hardly possible. Many instances were noted where the range of one type overlapped that of another, and a few cases were observed in which appendages of two distinct types occurred on an individual thallus (Figs. 15, H, I; 17, A, B). It was impossible, moreover, to associate the differences in the appendages with other differences showing any degree of constancy. In the writer's opinion, therefore, the numerous types of appendage are to be regarded as a further evidence of the great variability of the species.

In the case of the involucres there is again great variability, although the extremes are perhaps less marked than in *M. domingensis.* Fig. 20, L, shows an involucre in which the teeth are scattered, short, and blunt; while in Fig. 20, J, K, M, the involucres shown bear crowded, long and slender teeth. It will be noted that some of the teeth are simple while others are more or less complex. Bifid teeth are especially common and often show widely divergent divisions. The involucres are firmer than in *M. domingensis,* the cell walls being sometimes distinctly thickened and pigmented with yellowish brown.

In North America the only species with which *M. chenopoda* is likely to be confused is *M. domingensis.* The two species are of about the same size, the structure of the epidermal pores is much the same in both, the sclerotic cells in the ventral portion of the thallus show a similar distribution and the male receptacles are very much alike in general appearance. There are, however, striking differences which usually make it possible to distinguish specimens even in the absence of female receptacles. In *M. chenopoda* slime cells can almost always be observed in the thallus and often occur in great abundance; the appendages of the ventral scales are often entire and are never very closely toothed; and the stalk of the male receptacle is destitute of air-chambers. In *M. domingensis* there are no slime cells in the thallus; the appendages of the ventral scales are closely toothed; and the stalk of the male receptacle bears a band of air-chambers.

If female receptacles are present other important differences may be observed. In *M. chenopoda,* the stalk bears two bands of air-chambers; there are normally only five lobes, these being very short; and the involucre is firm in texture, the margin varying from dentate to ciliate or laciniate. In *M. domingensis* the stalk bears a single band of air-chambers, there are usually

more than five lobes, these being more or less elongated; and the involucre is very delicate in texture, the margin varying from crenulate to short-ciliate.

The features which distinguish *M. chenopoda* from *M. domingensis* will distinguish it also from the South American *M. papillata.* Another South American species to which it may be related is *M. Bescherellei,* the appendages and involucres of which might easily come within the range of variability exhibited by *M. chenopoda.* According to our present knowledge, *M. Bescherellei* is a more delicate species with lower air-chambers and thinner ventral tissue. There is no danger of confusing *M. chenopoda* with any of the other species recognized in the present paper.

Doubtful Species

1. Marchantia squamosa Raddi; Lehm. & Lindenb. in Lehmann, Pug. Plant. 4: 12. 1832 (as to the Brazilian plant).

Brazil: without definite locality or date, *Raddi.*

Attention has already been called to this species and to its possible aggregate nature (see p. 261). Stephani's description agrees in most respects with *M. paleacea,* and it is possible that Raddi's specimens would now be referred to that species. If this should prove true it would mark an interesting extension of range.

2. Marchantia quinqueloba Nees, Naturg. Europ. Leberm. 4: 98. 1838.

West Indies: without locality, date, or collector's name.

According to the full description given by Nees von Esenbeck this species is probably a form of *M. domingensis.* In any case there seems to be no reason for attempting to maintain it, since the original specimens (according to Stephani) are poorly developed and valueless.

3. Marchantia pusilla Nees & Mont.; G. L. & N. Syn. Hep. 526. 1847.

Chile: without locality, date, or collector's name.

This species was based on a single very immature specimen and is not represented in the Montagne herbarium. The original description throws little light on its affinities, and Montagne him-

self apparently had no faith in its validity since he does not mention it in his Sylloge (1856). Stephani therefore seems justified in repudiating it altogether.

4. Marchantia flabellata Hampe, Linnaea 20: 235. 1847.

Venezuela: Galipan, without date, *Moritz 47b* (erroneously ascribed by Hampe to Colombia).

According to the brief original account the species is monoicous, the female receptacles are four-parted, and the male receptacles seven-parted. Although no specimens have been available the writer suspects that *M. flabellata* may represent a synonym of *M. domingensis*. Should this be established it would show that Hampe confused the male and female receptacles and incorrectly assigned a monoicous inflorescence to his species. Unfortunately the question must be left in doubt.

5. Marchantia Notarisii Lehm. Pug. Plant. 10: 22. 1857.

Chile: near Valparaiso, without date, *W. Lehmann.*

Although Stephani at first threw doubt on the validity of this species, suggesting that it was probably synonymous with *M. chenopoda,* he afterwards listed it without question from the Chilean island of Chiloé, citing specimens collected by C. Skottsberg.[53] The original description of *M. Notarisii* is very full but is justly criticised by Gottsche[54] on account of its many ambiguities. It certainly seems to point to *M. chenopoda,* and the writer would refer it provisionally to that species. Unfortunately no specimens of *M. chenopoda* from Chile have been available for study.

Sheffield Scientific School,
Yale University.

[53] Kungl. Sven. Vet.-Akad. Handl. 46[9]: 5. 1911.
[54] Bot. Zeit. 16 (Beil.): 28. 1858.

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